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THE HIPPOBOSCIDAE OR LOUSE-FLIES (DIPTERA) OF MAMMALS AND BIRDS

PART I. STRUCTURE, PHYSIOLOGY AND NATURAL HISTORY

BY JOSEPH C. BEQUAERT

ALEXANDER AGASSIZ PROFESSOR OF ZOÖLOGY,
MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE,
CAMBRIDGE, MASSACHUSETTS

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“Blut ist ein ganz besondrer Saft.”
Goethe's *Faust*, Part I.

INTRODUCTION

The present work is the outcome of some thirty years' study of the dipterous family Hippoboscidae, the ectoparasitic louse-flies of birds and mammals, variously called also bird-flies, feather-flies, ked-flies or keds, spider-flies, tick-flies, and flat-flies. As originally conceived, it was to be only a taxonomic account restricted to the species occurring north of Mexico, for which area information is most complete. The Nearctic hippoboscid fauna is, however, so obviously an extension of that of the Neotropics, that eventually it seemed advisable to cover the whole of the New World. The larger scope will no doubt make the work more generally useful, while placing the North American fauna in its true perspective. On the other hand, I am only too well aware that the available Central and South American material is very scant, particularly in view of the well-known fact that the Neotropical bird fauna is richer than that of any other of the Earth's zoological areas. It is hoped, nevertheless, that in its present form the paper may be a safe working basis, as well as an incentive for future investigations.

The plan was at first that of my Monograph of the Melophaginae (1942a); but the introductory account of structure, function and bionomics has gradually grown into what purports to be a general Natural History of the Hippoboscidae, which is now published as Part I of the work. Several aspects of the structure, physiology and behavior of these insects are almost unique, so that they are of the greatest interest, particularly to the student of parasitism and evolution. Their study is also urgently needed, since many of these flies are doomed to extinction, with their hosts, in the near future. I have attempted to compile, to appraise critically from personal observations, and to correlate all published information on their outer and inner structure, physiology, ecology and behavior, calling attention meanwhile to the gaps that should be filled in by future research. Where information is either lacking or very scant for the louse-flies, I have sometimes referred to what is known of their nearest living relatives, particularly the tsetse-flies. Needless to say, it is not claimed that such information can actually be extended to the Hippoboscidae in every case.

It is not easy to write a properly balanced summary of a variety of subjects. Like every other naturalist, I have a weakness for certain topics, which is bound to be reflected in the disproportionate

extension given to certain sections. Other matters are more concisely treated, but I trust that no worthwhile contribution has been overlooked. I should also warn that certain publications, clearly out-of-date or obviously unreliable, have been deliberately neglected, although all are included in the Bibliography.

The general account of Part I called for so many references to papers not mentioned in the taxonomic bibliographies of Part II, that it was necessary to incorporate in the work a reasonably complete Bibliography of the Hippoboscidae to date.

In the taxonomic section forming the second part of the paper, the key to the genera of the Hippoboscidae of the World which I recognize as distinct, is designed for identification purposes only. It gives no clues to the true relationships, which are discussed in the chapter on "Relationship and Classification." Much effort has gone into preparing detailed generic descriptions, on a comparative basis, as none of those published to date are either reliable or adequate. A careful analysis of generic structure is, in my opinion, essential not only for the study of evolution within the family, but also for evaluating the true specific characters within each genus. I have been led to suppress some of the genera accepted thus far, since they were clearly based on characters which, though readily observable, are nevertheless trivial in the family as a whole.

Complete bibliographies of previous writings are given under each species, nearly all citations having been compared with the originals. Each citation also mentions briefly the most important information it contains, particularly all new localities and hosts, except for my own papers, since their contents are included in the text. Thus the bibliographies give credit where it is due and reflect the vicissitudes in the gradual growth of our present knowledge. Slow but steady accretions from many sources is an outstanding historical feature of Entomology. Each addition may be trivial by itself, but the sum total is often impressive, as is perhaps shown by the present memoir.

No new detailed descriptions of species were drawn up. Instead, the keys to the species include nearly all the characters believed to be fully reliable for diagnosis. Together with the illustrations, they should suffice for identification; but some additional features of minor value have been mentioned in discussing the affinities. Copies of the original descriptions, if needed in English translations, except for the Latin texts, have been appended, as well as remarks on the type specimens whenever these were available.

The paragraphs entitled "Distribution and Specimens Examined" detail under each species the localities and hosts from which I have seen material. In addition to new records, they include those published previously (as cited in the bibliographies), when I was able to study the specimens. Inasmuch as I have given full credit to earlier work, I feel that I do not infringe on other people's rights if I claim the responsibility for the identification of all specimens I have studied myself. In some cases the published records needed correction, while in others they were based in the first place on my own identifications.

When the species or subspecies of the host is definitely known, I use as a rule its scientific name in the body of the paper. As the vernacular names of birds and mammals are in more common use, particularly in Canada and the United States, there might have been some advantage in using these instead. English or other vernacular names, however, could only be confusing if used for foreign or tropical hosts; even some of the American names might be meaningless or misleading to British readers. Vernaculars will be added to the scientific names in the "Systematic List of the Hosts and their Parasitic Flies" which will conclude the second or taxonomic part.

Another concluding section will list the American species of flies according to geographical areas, political divisions (including the provinces and states of Canada and the United States) being used for convenience. A more detailed discussion of several aspects of distribution in the Americas will then be presented.

The following information is inserted in square brackets in the text. 1. Entries in the bibliographies that do not conform to binomial nomenclature, such as *nomina nuda*, pre-Linnaean citations, vernacular names, etc. 2. Information received from correspondents, but not confirmed by personal examination of specimens. 3. Explanatory words or remarks inserted in the copies or translations of original descriptions, more particularly the metrical equivalents of non-metrical measurements.

Measurements. In the Hippoboscidae size is in most cases a fairly reliable specific character, varying within rather narrow limits. The total length of the body is, however, of no significance, as the soft integument of the abdomen is expansible; in the same individual it is strongly contracted and hence very short upon emerging from the puparium, but increases greatly in size after feeding or, in the female, during the intra-uterine growth of a larva. The abdomen also shrivels after death, particularly in dry,

pinned specimens. Only two mensurations of length are fully trustworthy and comparable: the combined length of head and thorax, taken from the tips of the apical arms of the frons to the hind margin of the scutellum; and the length of the wing, taken from the base of the tegula to the tip of the membrane. The proportion of the greatest width of the thorax (before the base of the wing) to its median length (from the anterior margin to the hind margin of the scutellum) is also of some value, as well as the greatest width of the wing. The proportions of length to greatest width of the head and of the interocular face are also frequently used; but some judgment is needed in determining them. In specimens pinned after being kept for some time in a liquid, the face or eyes often shrivel or shrink from the original width in life. The length (or height) of the head should be measured from the tips of the apical arms of the frons to the occipital margin of the postvertex; while its greatest width is the distance between the extreme outer sides in front view, usually the outermost bulges of the eyes. The interocular face is the area bounded by the inner margins of the eyes, its length being that of an inner eye margin; its width, or horizontal distance between the inner eye margins, usually varies at different levels, the margins being rarely parallel; consequently, it is necessary to indicate the level at which the width was measured. The correct length and width of head and thorax and the proportions between them should be determined on specimens not mounted on slides. Slide mounts are more satisfactory for wing measurements. Most measurements vary individually in the same species within extremes of one-half to one millimeter; so that an approximation of half a millimeter is satisfactory for most purposes.

Collection and Preservation. Collecting Hippoboscidae presents special difficulties for the average entomologist, so I offer no apology for the following suggestions. Occasionally a stray specimen may be collected away from a host or newly emerged flies may be seen flying, particularly species of *Lipoptena* which sometimes swarm in numbers in search of a host. Such forms as the *Melophagus* of sheep, *Lipoptena* of goats, and *Hippobosca* of horses, cattle, camels and dogs, may be collected without much trouble from their domestic hosts; it is relatively simple to obtain *Pseudolynchia canariensis* and its puparia from domestic pigeons or in pigeon lofts. Some Old World species of *Ornithomyia*, *Crataerina*, and *Stenepteryx* may be bred from puparia found in birds' nests; this is hardly ever possible in the New World. *Olfersia* is sometimes abundant in or near the rookeries of certain marine bird hosts. The net re-

sults of such random collecting are practically negligible, as shown by the scarcity of louse-flies in the average dipterist's or museum collection. Incidental captures can never give a complete insight into the local hippoboscoid fauna and its relations to the hosts. During the many years I have been interested in these flies, I have collected personally very few of them, possibly not more than 1 or 2 per cent of the total number of specimens I have used for my work.

The student of the louse-flies must enlist the assistance of ornithologists, game-wardens, wild-life experts and hunters, a problem in human relations which he will have to solve as best he can. Personally I have usually found in such quarters the greatest willingness to help. It is particularly recommended to establish friendly contacts with organizations or persons engaged in the banding (or ringing) of birds. Juvenile birds usually predominate among birds trapped for banding during the fall migration and they are often more heavily infested than the older birds of the same species. Some further remarks on bird banding in relation to the study of the Hippoboscidae will be found in the introductory paragraphs of the section on the host-parasite relation. As was first pointed out by H. S. Peters (1930), the systematic and extensive trapping of live birds offers unusual opportunities for the study of many little-known aspects of hippoboscoid natural history. Latterly Mr. I. B. Tarshis has made extensive use of the method in studying the two flies of quail (*Lophortyx*) in California, *Lynchia hirsuta* and *Stilbometopa impressa*. His results were so far-reaching that I urged him to publish a detailed description of the two types of portable cages he devised for the examination of trapped quail in the field. With Mr. Tarshis' permission, general views of these cages are reproduced (Figs. 1 and 2). Instructions for their construction and use will be found in his recent paper (1952). A simple, but very efficient method of collecting a bird's flies without harming it was developed recently by K. Williamson (1952) at the Fair Isle Bird Observatory, Scotland. The live bird is immersed in a bath of chloroform fumes whilst keeping its head clear by means of a cape of oiled silk. It is the only method which provides data suitable for a statistical analysis of fly populations (Butterfield, 1952).

Young waders and birds of prey are sometimes banded in the nest; but most flies of large hosts must be obtained from killed birds; unless trapping can be used, this is at present the only available method for those of tropical birds and of wild mammals. Fully-winged flies usually leave the host shortly after its death or

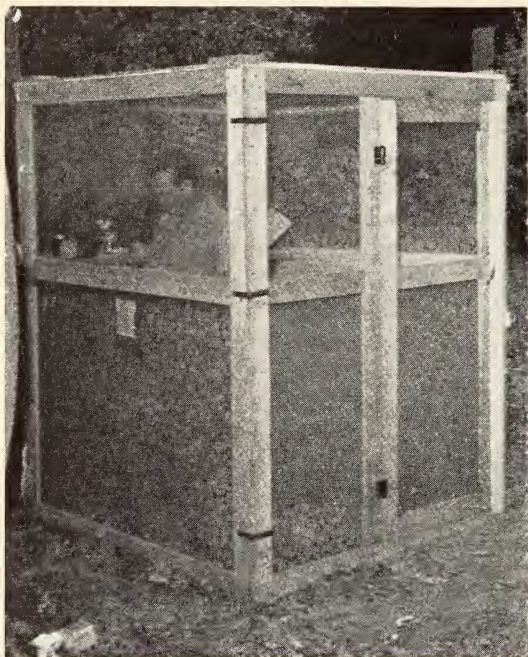


FIG. 1. Large portable insectary for collecting hippoboscids on live birds in the field. From I. B. Tarshis (1952, p. 71).

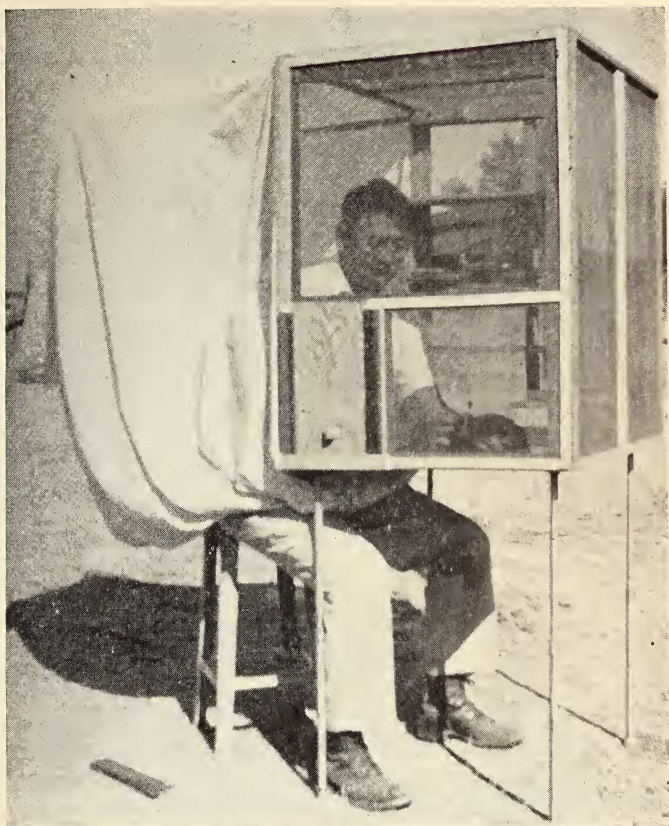


FIG. 2. Small portable insectary for collecting hippoboscids on live birds in the field. From I. B. Tarshis (1952, p. 77).

even while it is dying. They may also, in addition, move so swiftly among the feathers or hairs that they are likely to dodge the collector's fingers. In order to reduce losses to a minimum and to make sure of the correct host, it is strongly recommended that each bird be tied up as soon as possible after death in an individual strong paper or cloth bag of suitable size. Either the contents should be exposed to ether or chloroform fumes before opening the bag, or, better yet, the untreated bag should be opened indoors and the bird examined near a closed or screened window. A fly that leaves the body will usually dart for the screen or glass pane, where it can be stuck to a moistened finger and washed off directly in a vial of alcohol. In the field, hosts may be examined inside a mosquito bar with a very fine mesh. Occasionally a fly may remain on a dead bird for several hours and be found while preparing the skin. When several birds of different species lie about during the skinning process, flies may easily move from one bird to another, so that records obtained under such conditions are often questionable. This is even more true when hosts of several species are brought in from the field in the same bag or container, a frequent source of erroneous host records. Sometimes a fly, after leaving a dead or dying bird, is unable to find a new live host and eventually returns to a dead bird, either the one it had just left or some other one lying near it. Flightless hippoboscids tend to remain on dead hosts much longer than fully-winged species.

For best results in later studies, the flies should be dropped as soon as possible after capture in 75 to 80 per cent clean, unadulterated ethyl alcohol, and be properly labelled with locality, date, name of collector and of host. It is better not to add glycerine to the alcohol, as this may interfere with later study. The name of the host should be given as accurately as possible and preferably obtained from a competent ornithologist or mammalogist. If the skin of the host is preserved, its serial number should be given on the label of the fly so that the name of the host may eventually be verified. These precautions are most important in tropical areas, where many birds are as yet imperfectly known and their parasites even less. Since no stoppered vial has yet been devised from which alcohol will not evaporate eventually, the vials should be plugged with cotton and permanently kept immersed in alcohol in larger containers in the museum.

Dry, pinned specimens of known species can usually be correctly identified. However, they show rarely all the specific characters clearly, particularly those of the abdomen, which is often

shrivelled to such an extent that even the sex can no longer be determined. Even prolonged soaking, boiling, or maceration usually fail to soften the dried abdomen and to restore it to the original shape. I advise against mounting hippoboscids on slides, either in Canada balsam or in some other medium, after softening and clearing the specimens by maceration and removal of the inner tissues. Such manipulations are apt to remove or distort certain delicate outer structures, while making visible by transparency various inner structures, apodemes and ridges, which may be readily mistaken for outer structures. On the other hand, the true surface limits of the sclerites and the true external structures may become obliterated, or some of the characteristic chaetotaxy may be lost. Furthermore, it is nearly impossible to determine with any degree of accuracy from a fly mounted under a cover glass the original proportions of the several external body areas, notably those of the interocular face. Cleared specimens are useful only for the special investigation of certain minute structures and even then should be used with extreme care, lest they lead to erroneous conclusions. A case in point is the determination of the number and location of the abdominal spiracles, which seem to be easily removed with the tracheae by the clearing manipulations. I was privileged to examine slides of several species of *Ornithoica* prepared some years ago by an experienced entomologist. Although it was eventually possible to locate all seven pairs of abdominal spiracles by combining the findings on all the slides, no single slide showed the full set and some showed none at all.

Personally, I am reluctant to describe a new species of hippoboscid solely from either a dry and pinned specimen or a slide mount. Much of the difficulty in recognizing the true identity of the types of earlier authors lies in their being poorly preserved, pinned specimens, on which some of the essential specific or even generic characters cannot be seen.

An additional word of caution to the beginner may be pertinent, since it is hoped that the present work will be the incentive for a renewed interest in the Hippoboscidae. He should be wary of regarding as a novelty any specimen that seems to depart from the published figures and descriptions of the known species. Quite apart from individual intraspecific variation, which may be wider than suspected or recognized, the condition, age or method of preservation of the specimen may be deceiving. Published information also may be not fully reliable and even drawings by reputed and skilful workers may be misleading. My long experience with the

Hippoboscidae leads me to believe that the probability of a beginner's finding an undescribed species in a limited material is very small and I should think nil for the United States and Europe. If anyone wishes to "split" the now recognized Nearctic and Palearctic species, or to subdivide them into subspecies, he should choose names from among those now stored in the synonymy, rather than invent new ones.

The descriptions and original drawings in the present work were made by the author almost exclusively from alcoholic material. This was left to dry just enough to disclose the limits of the sclerites, the sutures and the insertion of the setae under the dissecting, binocular microscope. Care should be taken to keep the specimen sufficiently moist, so as to prevent the appendages from becoming brittle and the abdomen from shrivelling. Illustrations copied or adapted from my predecessors, as far as possible with their permission, have been fully credited to them.

Acknowledgments. I have been more than usually fortunate in enlisting the assistance of many entomological colleagues, ornithological friends, game-wardens, museum curators and even casual acquaintances, all of whom have provided specimens or information. Their names will be listed at the close of Part II; at present I wish to thank them collectively for their kind and generous help.

To the following persons I wish to express my appreciation for special contributions to various sections of Part I. Mr. Irvin Barry Tarshis, of Berkeley, California, has most generously communicated some of the unpublished results of his researches on the bird-flies of quail, and I am also indebted to him for many other favors. I have likewise been privileged to read in manuscript the important observations on the pigeon-fly by Dr. J. H. Schuurmans Stekhoven and his co-workers at the Fundación Miguel Lillo of Tucumán, Argentina, which are to appear shortly and perhaps even before my own work. Information obtained from both these sources has enabled me to put some earlier published contributions in the proper perspective. Relatively little of this unpublished work, however, has been mentioned in my paper, with the authors' permission, as I did not wish to detract from the originality of their forthcoming publications.

I am indebted to Dr. B. Jobling, The Wellcome Research Laboratories of Tropical Medicine, London, England, not only for permission to reproduce some of his published figures, but also for advice on moot problems of anatomy and particularly on the true

homologies of frons and clypeus; Figs. 6E-F are from his original unpublished drawings. Dr. J. E. Webb, University College, Ibadan, Nigeria, and the Zoological Society of London have kindly allowed me to copy the illustrations in Fig. 16. Similar permission was granted by Mr. K. MacArthur and several other persons as well as Institutions, as mentioned in the explanations of some of the figures.

Dr. Clay G. Huff, Naval Medical Research Institute, Bethesda, Maryland, and Dr. G. Robert Coatney, National Institutes of Health, also at Bethesda, have offered valuable suggestions in discussions of the development of pigeon malaria and similar blood parasites. Professor H. R. Hagan, College of the City of New York, read critically the section on the embryology and early development, and Dr. Kenneth W. Cooper that dealing with the chromosomes. Much of the information on the Laboulbeniaceae was obtained from Mr. Richard K. Benjamin, while he was a Graduate Student at the Biological Laboratories of Harvard University. In connection with these fungi, I received valuable help also from Mrs. F. L. Balfour-Browne, at the British Museum (Natural History).

Mr. G. B. Thompson, Cambridge, England, has for many years been most generous in communicating interesting material and valuable information, particularly on publications otherwise inaccessible. Dr. F. I. van Emden, British Museum (Natural History), and Mr. E. Séguy, of the Paris Museum of Natural History, have contributed much time and advice, either during visits to study the collections in their care or by correspondence. I owe a special debt of gratitude to Mr. James E. Collin, Newmarket, England, for his unfailing assistance in answering my repeated inquiries and more particularly for his kind hospitality while studying the valuable types of Bigot's Hippoboscidae at his home in September, 1951.

It would have been utterly impossible to attempt an intelligent discussion of the host-parasite relation of the Hippoboscidae, one of the major sections of this work, without the continued help and suggestions of several ornithologists and mammalogists here and abroad. I wish particularly to express my appreciation to my lifelong friend, Dr. James P. Chapin, The American Museum of Natural History, New York, who devoted much time to a criticism of parts of my manuscript dealing with ornithological matters. I am also under special obligation to my colleagues at the Museum of Comparative Zoölogy, the late James Lee Peters, Mr. James C. Greenway, Mrs. Barbara Lawrence Schevill, and Dr. Charles P. Lyman.

Finally, I wish to express my gratitude to the Treasurer and the Publication Committee of the Brooklyn Entomological Society, whose generous and sympathetic interest made possible the publication of this work in its present form.

EXTERNAL ANATOMY

The following account of the external anatomy has a threefold purpose. It intends first to define the terms used in the taxonomic discussions for the several parts or areas of the exoskeleton. It attempts also to trace, in so far as possible, the homologies of these parts in the Hippoboscidae with those of other related Diptera. Finally it explores the most important modifications within the group, preliminary to a discussion of the relationships of the subfamilies and genera.

In tracing the homologies and in selecting and defining the terms, an earnest attempt has been made to adopt the latest findings of comparative insect anatomy. The professional morphologist is prone to decry the non-morphological terminology used in the Diptera by the average taxonomist, whom he seems to regard as a mere willing victim of mental sloth. After spending many tedious hours on a variety of morphological writings, I have reached the conclusion that a reasonably stable terminology, based on the true homologies and applicable to all parts throughout the Order Diptera, is as yet a hopeful dream. Morphologists disagree among themselves to such an extent that the unbiased outsider is often at a loss to decide which point of view to adopt. Their involved discussions of moot points sometimes raise the suspicion that they are perhaps not quite so sure of their ground. Meanwhile the taxonomist must use a certain term with a definite meaning and cannot well wait until the morphologists have settled the matter or change his terminology every other year. With regard to the Hippoboscidae in particular, the morphologists usually stop so far from the goal that they are of little assistance in deciding which terms to adopt. Moreover, I am by no means convinced that, in such highly specialized insects as the ectoparasitic Diptera, it will ever be possible to trace the true homologies of all the parts. Sometimes one interpretation seems to carry as much weight as another, in which case it may be better to "accept the facts as they are" (R. E. Snodgrass) and to adopt conventional terms, which at least have the advantage of not implying more knowledge than is actually attainable.

Anticipating a later discussion of the affinities, it may be helpful to state at the outset that the term "Diptera Pupipara" (or

"Pupipara" for short) will be used as a convenient collective name for the Hippoboscidae, Streblidae and Nycteribiidae, the only dipterous families of permanent ectoparasites with integral viviparity (so-called pupiparity). It does not intend to cover a taxonomic category nor to imply any close relationship or common origin. The Hippoboscidae will be divided in the present paper into six subfamilies, two of them, the Ornithoicinae and Ornithomyiinae, being restricted to birds and four, the Hippoboscinae, Melophaginae, Ortholfersiinae and Alloboscinae, to mammals (except for *Hippobosca struthionis* of the ostrich).

In order to trace the homologies, I have used for comparison the head and thorax of one of the Glossinidae or tsetse-flies, *Glossina fusca* Walker, original drawings of which are included. Among the higher Muscoidea, these flies appear to be structurally most similar to the Hippoboscidae and possibly their closest living relatives.

The structure of the head and thorax of the Hippoboscidae is most readily understood if the adult fly is conceived as a dorso-ventrally flattened, blood-sucking, higher muscoid. The hippoboscid head capsule was first explained on this assumption by B. Jobling (1926, p. 329; with a useful diagram, text-fig. I). In addition, certain areas or parts of the exoskeleton have been modified, mainly by fusion, reduction or atrophy, in response to permanent ectoparasitism. The dorso-ventral flattening is less apparent in the abdomen, due to the reduction of the sclerotized areas, itself correlated with the peculiar viviparous mode of reproduction.

The head (Fig. 3A-C; *Microlynchia pusilla*) is clearly a strongly flattened muscoid head, in which several of the original areas may be recognized without much difficulty. The upper surface either is horizontal or slants slightly downward and forward. The head shows none of the extreme modifications of the Streblidae and Nycteribiidae and its structure is fairly uniform throughout the family. That of the most highly specialized genus, *Melophagus*, may be tied up through the related *Lipoptena* with that of the more generalized *Ornithomyia* and *Ornithoica*. The relative uniformity of the head and its appendages, particularly the mouth-parts, points strongly to a monophyletic origin for the entire family. Owing to the dorso-ventral flattening, the mouth-parts are directed forward, not downward as in the Muscoidea, the head being of the prognathous type. As in all Myiodaria, the *occipital foramen* (*OCF*) is relatively small and occupies a median or submedian position on the hind part of the head, which is connected with the

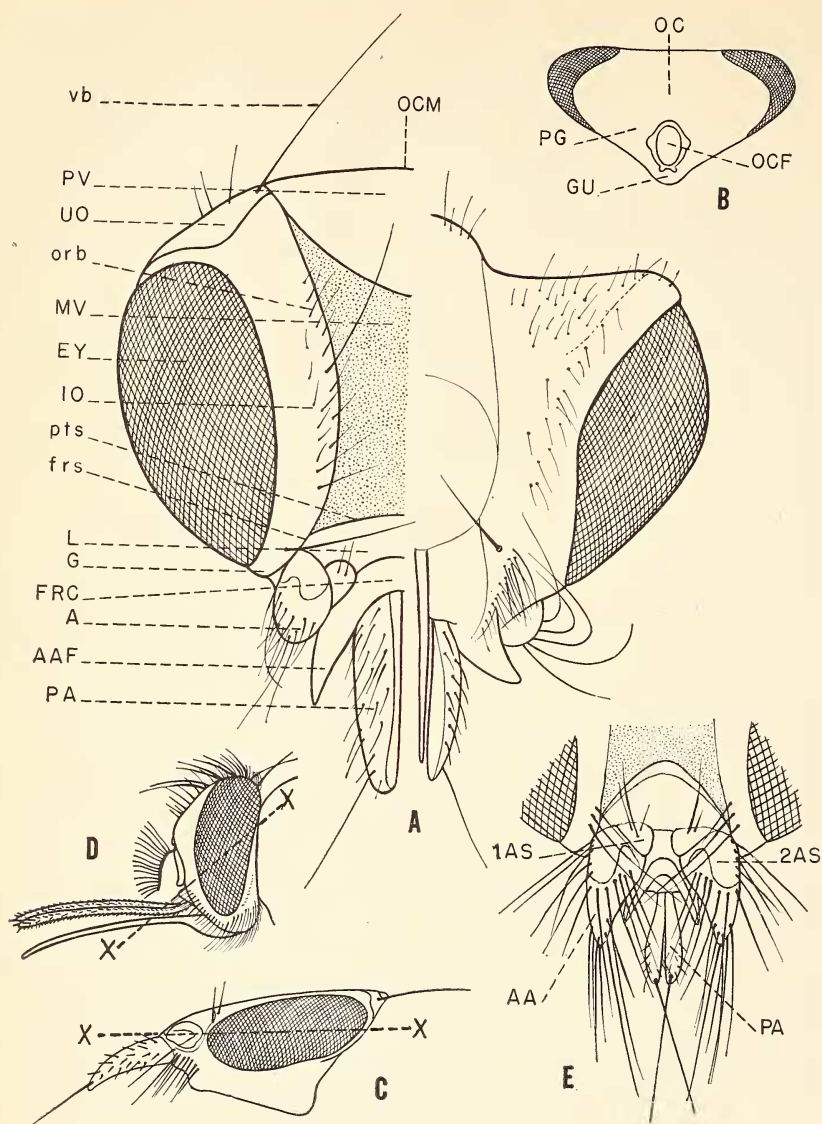


FIG. 3. A-C, *Microlynchia pusilla* (Speiser), female; head from above and below (A), from behind (B) and in profile (C): A, antenna; AAF, apical arm of frons; EY, eye; FRC, frontal carina; frs, frontal suture; G, gena; GU, gula; HA, haustellum; IO, inner orbit; L, lunula; MV, mediovertex; OC, occiput; OCF, occipital foramen; OCM, occipital margin; orb, orbital bristles; PA, palpus; PG, postgena; pts, ptilinal suture; PV, postvertex;

prothorax by means of a short and narrow membranous neck. I fail to see, however, that the neck is much more reduced than in other Diptera (including the Myiodaria) with a freely movable head.

In the Hippoboscinae the head is rounded posteriorly and entirely free from the thorax, with a distinct intervening pronotum (Fig. 11E, *PT*), so that it can move not only up and down, but also sideways. In all other Hippoboscidae the hind margin of the head juts against the more or less concave, or at least depressed, anterior margin of the thorax. The connection between head and thorax is rather loose in the Alloboscinae, Ortholfersiinae, Melophaginae and Ornithoicinae, in which the humeral callosities form short and broad lobes, similar to those of the Muscoidea, allowing the head some free lateral motion. In the Ornithomyiinae, however, the humeral angles of the callosities are long and point forward, flanking the sides of the head in such a way that it can no longer move sideways. In extreme cases (*Crataerina*, *Stenopteryx*, and *Myiophthiria*) the head fits so snugly in the thorax that the two form as it were a single streamline unit, at least for motion in one plane. Such an arrangement has obvious advantages for scurrying amidst the feathers of avian hosts. It is therefore noteworthy that the most evolved cephalo-thoracic connection is found only among some of the bird parasites and is most perfect in the flies of swifts and swallows; while the more primitive condition of a freely movable or loosely attached head occurs, with the exception of the Ornithoicinae, among the parasites of mammals.

The most important landmark on the dorsal surface of the head, or *face*, is the conspicuous, transverse, more or less crescent-shaped *ptilinal suture* (*pts*), which marks the fissure where the inflated *ptilinum* (*pt*; ptilinal sac) retracts within the head capsule after the fly emerges from the puparium. The ptilinum is no less developed in most Hippoboscidae than in other Schizophora; but owing to the flattening of the head and the strong scleriosis of the frons and inner orbits, the edges of the ptilinal suture fit together very tightly. The ptilinal suture divides the median portion of the face into an upper area or *vertex* (*V*; including the frontalia, parafrontalia and ocellar plate of authors) and a lower area or

UO, upper orbit; the combined mediovertex and postvertex is the vertex (*V*); *vb*, vertical bristle. **D**, *Glossina fusca* Walker, female; head in profile. The line *X—X* in **C** and **D** marks the level of the dorso-ventral flattening of the head. **E**, *Ornithomyia avicularia* (Linnaeus), female; frontal area and antennae: *AA*, antennal appendage; *1AS* and *2AS*, first and second antennal segments; *PA*, palpus.

frons (*FR*; clypeus of many authors; prefrons of Ferris, 1950; formerly called fronto-clypeus by Jobling, 1926; including the lunula, facialia and interfacialia or facial plate). Most characteristic for the Hippoboscidae is the flattened, near-horizontal frons, in the same plane as the vertex, the antennae being pushed forward to near the oral margin of the face. Within the family three types of frons may be recognized, here discussed somewhat in detail, because of their bearing on the evolution within the group.¹

1. The most primitive condition is found in the Ornithoicinae, a subfamily which on other grounds also appears to be more generalized than any of the other Hippoboscidae. In *Ornithoica* (Fig. 5C), the frontal area is essentially as in most Muscoidea, except for the horizontal flattening and the forward position of the antennae. The supra-antennal (or post-antennal) region, or *lunula* (*L*; frontal lunule, frontal crescent, or antennaria of authors), is moderately wide and alone visible between the ptilinal suture and the base of the antennae. The antennae are large, flat, covering much of the frons and placed in a single deep *antennal cavity* (facial depression, facial plate, or interfacialia of authors in Muscoidea). Both enlarged first antennal segments, recognized by the presence of a row of bristles, lie side by side, their inner margins touching without intervening *frontal carina* (facial carina in Muscoidea, of most authors), except for a very short, triangular area set off by a fine transverse suture from the lower edge of the lunula.

2. Variants of the next known evolutionary stage occur in the Ornithomyiinae. In *Olfersia* (Fig. 7F), *Lynchia* (Fig. 5A), *Pseudolynchia*, and *Microlynchia* (Fig. 3A), where it is most readily

¹ In a recent discussion of the structure of the insect cranium, Snodgrass (1947, p. 3) takes the view that the terms "frons," "vertex," "clypeus," and "genae" correspond to topographical and not to anatomical areas, so that a great deal of latitude may be allowed in their application to different types of insects. He is also of the opinion that most of the impressed lines or grooves on the surface of the head are not "sutures" in the true sense of the term, but merely "sulci" or furrows, incidental to the formation of secondary strengthening ridges on the inner surface of the exoskeleton. In the present discussion I have found it more convenient to adhere to the customary use of the term "suture" for most external impressed lines, regardless of their possible origin, which is frequently in dispute.

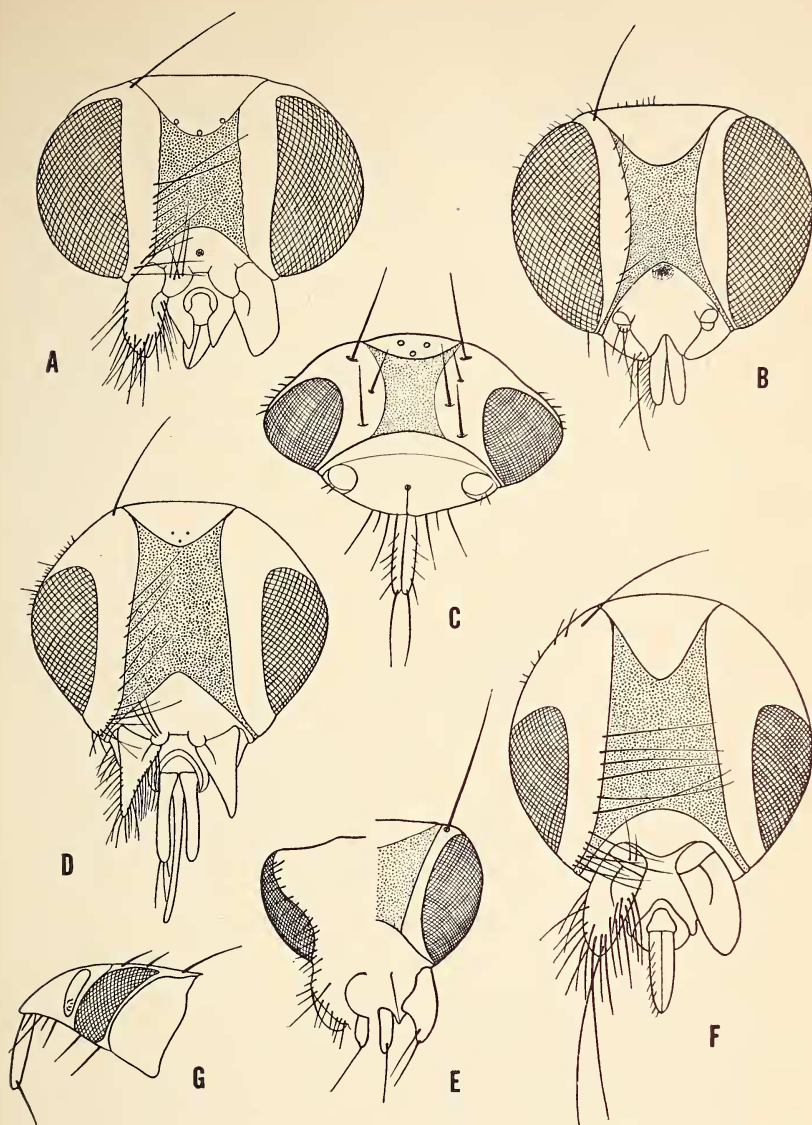


FIG. 4. Heads of Hippoboscidae: **A**, *Ornithoza metallica* (Schiner), female, from above. **B**, *Hippobosca longipennis* Fabricius, female, from above. **C**, *Lipoptena rusaecola* J. Bequaert, male, from above; **D**, *Stenepteryx hirundinis* (Linnaeus), female, from above. **E**, *Allobosca crassipes* Speiser, female, from above (at right) and below (at left). **F**, *Crataerina pallida* (Latreille), female, from above. **G**, *Lipoptena rusaecola* J. Bequaert, male, in profile.

studied owing to the small size of the antennae, the lunula, more extensive than in *Ornithoica*, occupies the major part of the frons; the bases of both first antennal segments are often fused with it, except at their inner and outer sides. In addition, the antennae are far apart and separated throughout by the widened, flattened, strongly sclerotized *frontal carina* (*FRC*). Apically this carina is deeply divided by a broadly triangular notch into long, diverging *apical arms* (*AAF*), while the basal, undivided portion may be depressed or grooved longitudinally; a distinct, complete transverse suture divides the lunula from the frontal carina. Each antenna lies in its own *antennal pit* (*AP*), open anteriorly, however, where the appendage of the second antennal segment extends beyond it. Narrow lateral extensions of the lunula, corresponding to the facialia of the Muscoidea, form the outer margins of the antennal pits. In other Ornithomyiinae, such as *Ornithomyia* (Fig. 3E), *Crataerina* (Fig. 4F), *Stenepteryx* (Fig. 4D), and *Myiophthiria*, the frontal carina is often nearly completely fused with the lunula, though abruptly narrowed at the base. In *Ornithoictona* the apical arms divide the frontal carina nearly to the base; in *Ornitheza* (Fig. 4A) they diverge at first, then converge again and run side by side before the tips.

3. The third and most derivative type is that of the Hippoboscinae (Fig. 5B), Melophaginae (Fig. 4C), and Ortholfersiinae. In these subfamilies the lunula and greatly widened frontal carina form a single sclerite, only slightly wider basally. The small antennae occupy the extreme lower corners of the frons, each in its own antennal pit, which is usually surrounded completely by a continuous rim (except in the Ortholfersiinae). In most cases the flaring apical arms of the frons are more or less developed, though rather short and widened basally. In the Melophaginae, by far the most specialized members of the family, the anterior (or oral) margin of the frons is broadly rounded off, with the barest trace of a median notch extended basad as a narrow, superficial furrow; very rarely there is a faint indication of a transverse line setting off the lunula above the antennae.

In some respects the Alloboscinae are intermediate between the second and third types: the frontal carina forms a broad, flattened plate, fused basally with the lunula, though abruptly narrower and sharply set off from both adjoining first antennal segments, themselves fused basally with the sides of the lunula; the antennal pits are incomplete anteriorly, the appendages of the second antennal segments extending far beyond them (Fig. 5D).

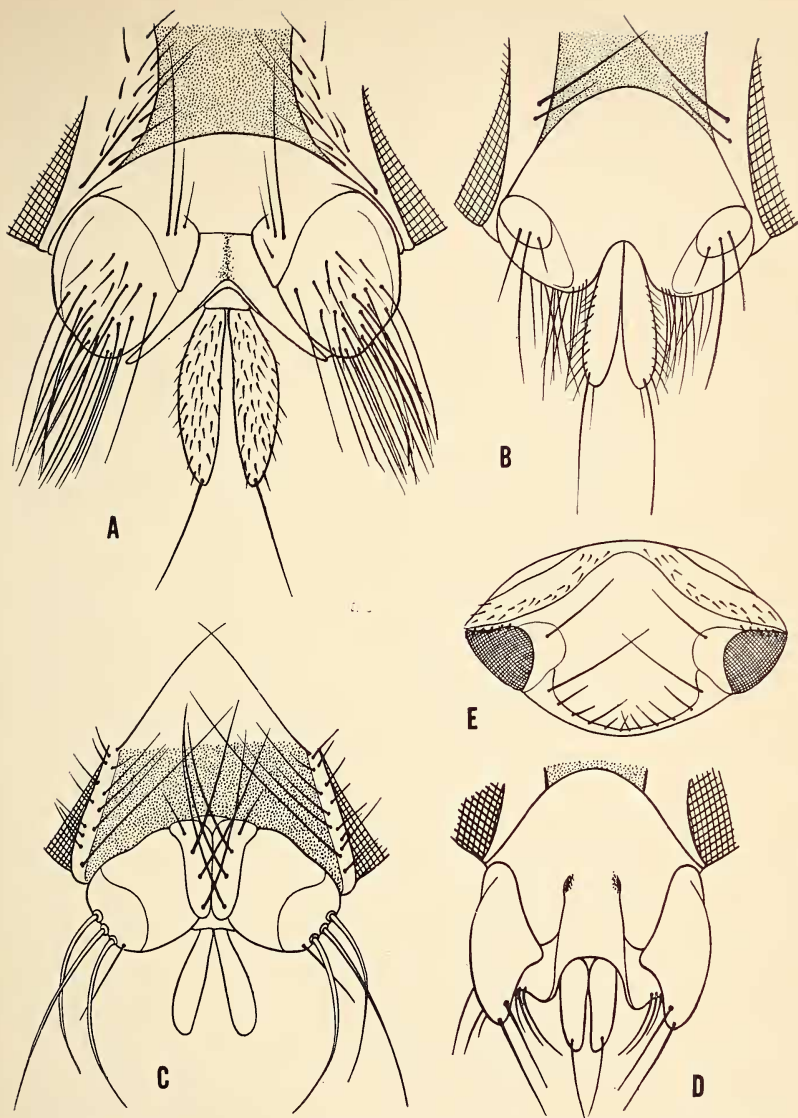


FIG. 5. **A-D**, Frontal areas and antennae of Hippoboscidae: **A**, *Lynchia albipennis* (Say), female. **B**, *Hippobosca longipennis* Fabricius, female. **C**, *Ornithoica vicina* (Walker), female. **D**, *Allobosca crassipes* Speiser, female. **E**, *Lipoptena rusaecola* J. Bequaert, male; head from below.

Some of the higher Muscoidea show indications of changes in the lunula and frontal carina which may help to understand the extreme modifications of the Hippoboscidae. In *Pollenia rudis*, the upper part of the frontal carina is distinctly widened between the antennae; moreover, the first antennal segment, although very small when compared to the second and third, is shaped much as in *Ornithoica*. The frontal carina is much more developed in several of the so-called bot-flies, unrelated higher Muscoidea parasitic in the larval stages on mammals, and particularly among the Cuterebridae and the Hypodermatidae. It reaches its extreme development in *Oestromyia*, where the antennal region of the frons is not unlike that of the more derivative Hippoboscidae: the frontal carina, completely fused with the lunula, is very broad, short and flat, with diverging lateral edges forming the inner rims of small, anteriorly open antennal pits.

Beyond and beneath the apical arms or edge of the frons may be traced the greatly reduced true *clypeus* (*CL*; anteclypeus or epistome of authors), on which the cibarial muscles are attached. It is usually in a ventral position and sometimes far back, as in *Melophagus*, where it lies near the middle of the ventral surface of the frons. The clypeus serves as a hinge for the rostrum of the proboscis and is connected by lateral sclerotized plates or bars with the cibarial pump. (Figs. 6E-F, drawn by Dr. B. Jobling).

A comparison of the frontal and clypeal areas of the higher Muscoidea and Hippoboscidae shows that the head of the latter is flattened approximately at the level of the line X—X in Fig. 3D of *Glossina fusca* and Fig. 3C of *Microlynychia pusilla*. The flattening results from an outward transverse fold of the integument running from the occipital foramen across the lower portion of the eyes to the ends of the lateral frontal sutures and to the lower margin of the frons proper (vibrissal angles of the Muscoidea). The area above the line X—X became a horizontal plane; that below the line folded backward and upward beneath the head, much of it providing the material for the soft rostrum membrane within which the proboscis may be retracted. The head is more flattened anteriorly than behind, so that it is triangular in profile and wedge-shaped (Figs. 3C and 4G), the keel-shaped anterior (frontal) margin being ideal for sliding forward amidst the plumage or pelt of a vertebrate host.

The upper part of the vertex is a median, strongly sclerotized, usually well-defined plate, the *postvertex* (*PV*; vertical triangle or ocellar plate of authors). It bears the three *ocelli* (*OCI*), when

these are present. The blunt or sharp edge between the postvertex and occiput is the *occipital margin* (*OCM*). The entire area of the face limited by the inner margins of the eyes is sometimes called the frons; but it is better referred to as the *interocular face* (*IF*; postfacial area of certain authors). It consists mainly of a median, generally soft, wrinkled portion, the *mediovertex* (*MV*; frontal vitta, frontalia, or interfrontalia of writers on the Muscoidea), with a rough surface of microscopic scales giving it a dull appearance. It is separated on each side from the eye by a narrow, hard sclerite, the *inner orbit* (*IO*; geno-vertical plate, parafrontal, or laterovertex of authors). *Olfersia* is unusual in that the ptilinal suture has moved so far back (or upward) that it divides the face into two nearly equal areas; the postvertex, devoid of ocelli, encroaches upon the mediovertex and often reaches the ptilinal suture.

The dorso-lateral portion of the head, behind each eye, is the *outer orbit* (*OO*), usually very narrow and sometimes lacking, particularly when the eyes extend over the ventral side. The upper area, above the eye, is the *upper orbit* (*UO*). The narrow lateral area, continuing the inner orbit between the lower border of the eye and the *frontal suture* (*frs*; lateral extensions of the ptilinal suture) is the *gena* (*G*; cheek or jowl of authors); although the extreme forward position of the antennae in the Hippoboscidae makes it impossible to distinguish the parafacial areas clearly from the genae. The hind or occipital surface of the head is divided by the *occipital foramen* (*OCF*) into an upper area, the *occiput* proper (*OC*), a lower area, the *gula* (*GU*), and two lateral *postgenae* (*PG*).

The *compound eyes* (*EY*) are as a rule large, always broadly separated in both sexes and with many small facets all of the same size. In some genera they are entirely dorsal, occupying the major part of the sides of the face. In the Ornithoicinae and Melophaginae they are, in addition, smaller and particularly narrower than usual. The smallest eyes, with the fewest ommatidia, are those of *Myiophthiria* and *Melophagus* (about 135 ommatidia in the latter). The surface of the eye is always bare. The development of the *ocelli* (*OCI*) varies greatly. In appraising evolutionary trends within the family their presence may safely be regarded as marking the more primitive types. In nearly half of the genera (8 out of 20) three ocelli are present, although they may be very small or vestigial in certain species. The majority of these genera are bird parasites of the subfamilies Ornithoicinae and Ornithomyiinae; but two of them are mammalian parasites of the

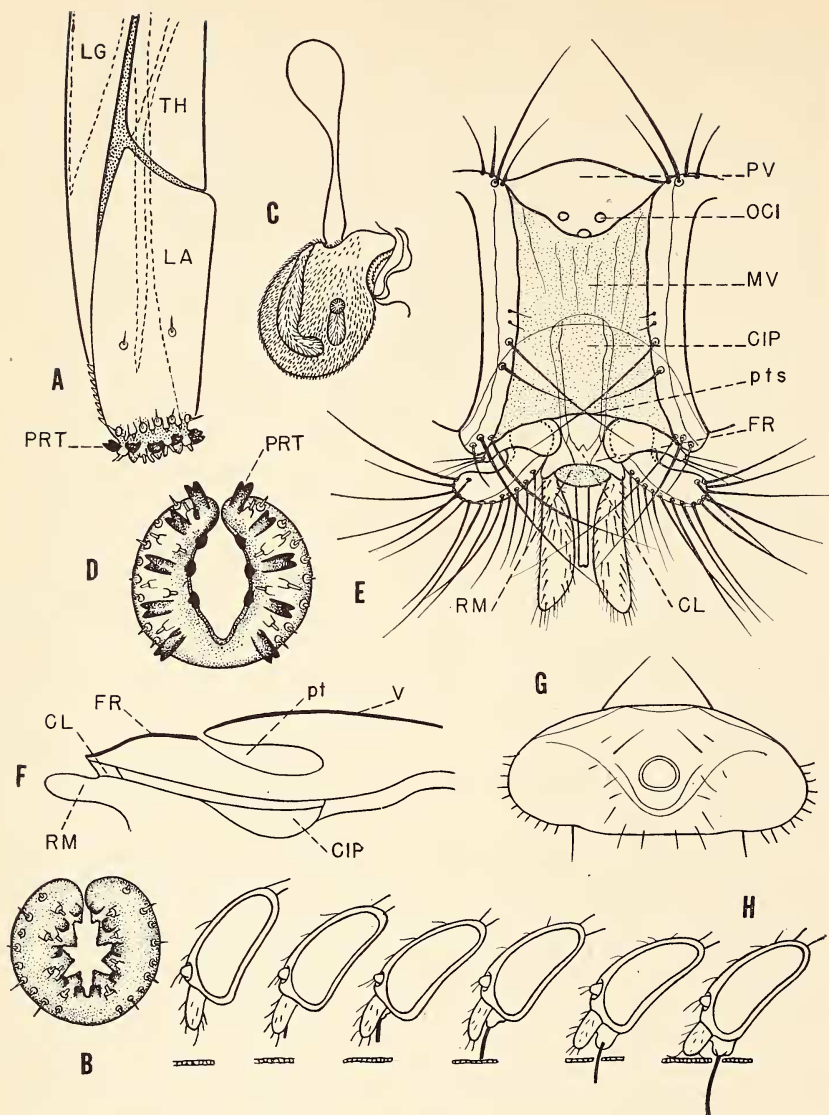


FIG. 6. **A-C**, *Pseudolynchia canariensis* (Macquart), after Jobling (1926): **A**, tip of haustellum in side view, showing labella (*LA*), ends of labial gutter (*LG*) and of theca (*TH*), and all prestomal teeth (*PRT*) everted. **B**, end view of labella with two sets of prestomal teeth inverted. **C**, third antennal segment and arista removed from cavity of second segment. **D**, *Hippobosca equina* Linnaeus; end view of labella with two sets of prestomal teeth (*PRT*) everted, after Jobling (1926). **E-F**, *Ornithomyia avicularia* (Linnaeus), after

subfamily Melophaginae. Of the remaining 12 genera, 11 are always without even traces of ocelli, 5 of these occurring on birds and 6 on mammals. The lack of ocelli is the invariable rule among the mammal-inhabiting Hippoboscinae, Alloboscinae and Ortholfersinae. The Melophaginae alone among the parasites of mammals contain both genera with and without ocelli. In the Ornithomyiinae, the genus *Lynchia* is aberrant in that most of the species are entirely without ocelli, while a few show more or less distinct vestiges of them and some (subg. *Ornithophila*) even have them fully developed. In *Ornithomyia*, on the other hand, most of the species have distinct ocelli, but in a few (subg. *Pseudornithomyia*) these organs are atrophied. Attempts have been made to correlate the atrophy or loss of ocelli in the Hippoboscidae with the reduction of the compound eyes and also with the loss of the power of flight (Massonat, 1909). There are, however, many exceptions to these supposed correlations, *Olfersia*, *Pseudolynchia*, *Stilbometopa*, *Ortholfersia*, and *Hippobosca* being all without even traces of ocelli, yet fully-winged and active fliers, with large compound eyes. Nevertheless, it might be of some significance that, of the five genera in which the wings are either atrophied, reduced or lacking, only one (*Stenopteryx*) has retained ocelli, moreover of small size or vestigial. There is also a possibility that even in some of the Hippoboscidae with ocelli, these organs may be functionless, since they are frequently very small and flat. In insects in general the function of the ocelli is controversial. From their structure they cannot receive an image; most likely they merely register changes in intensity of illumination. This might be of some assistance before and during flight by accelerating the insect's response to shadows and by keeping the body back uppermost (Kalmus, 1945; Parry, 1947).

The *antennae* (A) are, with the male terminalia, the most modified external organs of the Hippoboscidae; yet it is possible to homologize their structure without much difficulty with that of the higher Muscoidea. They are apparently immovable, placed far forward, near the apical margin of the frontal area, and in most

original sketches by Dr. Jobling: **E**, interocular face and frontal area from a cleared specimen mounted on a slide without any pressure on the cover slip; **F**, ideal cross-section of anterior portion of head: *CIP*, cibarial pump with lateral plate or bars; *CL*, clypeus; *FR*, frons; *MV*, mediovertex; *OCI*, ocelli; *pt*, ptilinum; *pts*, ptilinal suture; *PV*, postvertex; *RM*, rostrum membrane; *V*, vertex. **G**, *Lipoptena rusaecola* J. Bequaert, male; head from behind. **H**, *Hippobosca equina* Linnaeus; 6 successive stages of the biting process, in side view, after Hase (1928).

cases (except in *Ornithoica*) well separated by the flattened frontal carina. In *Ornithoica* they lie in a single frontal cavity; in the other genera each of them has its own deep *antennal pit* (*AP*), surrounded by a partial or complete rim. The *first antennal segment* (*1AS*; scape) is readily recognized in the more primitive *Ornithoica* (Fig. 5C), where it is large and flattened, completely separated by a deep suture from the lunula, and with strong setae as usual in the higher Muscoidea. In most other genera it is more or less fused with the sides of the lunula, although its position may often be traced by the characteristic setae. In the Melophaginae, there is no external indication of this segment; according to Jobling, in *Melophagus ovinus* it is deeply merged in the head capsule and its dorsal part, overlapped by the anterior border of the antennal pit, is devoid of setae. The *second antennal segment* (*2AS*; pedicle) comprises the major part of the antenna, being much flattened. Ventrally it is hollowed out into a pouch containing the greatly reduced *third antennal segment* (*3AS*; flagellum), hidden from view except for the protruding *arista* (*AR*). The shape of the second segment varies greatly and will be described under the several genera. In the Ornithoicinae (Fig. 5C) and Ornithomyiinae (Fig. 11F), the dorsal face of the second segment is extended into a flattened prolongation, the *antennal appendage* or process (*AA*), always bearing many setae and bristles, particularly at the apex. The extreme development of these appendages is reached in *Ornithoctona* and its subgenus *Ornithopertha*. The Ortholfersiinae have small antennal appendages, while in the Alloboscinae (Fig. 5D) they are of a peculiar form. In the Hippoboscinae (Fig. 5B) and Melophaginae (Fig. 4C), the second segment lacks the appendage, being small, subglobular, only partly filling the antennal pit. The *arista* (*AR*) of the third segment varies in shape, spatulate at the tip in *Ornithoica*, *Ornithomyia*, and *Pseudolynchia* (Fig. 11F), dichotomously branched in *Hippobosca*, bifid with comb-like branches in *Melophagus*, and variously divided in other genera.

In nearly all true Muscoidea Calyptrata the dorsal surface of the second antennal segment shows at least a trace of a longitudinal slit or furrow extending some distance from the apical margin. The slit is lacking in all true Acalyptrata. This character is regarded by many dipterists as of paramount importance in classification and in tracing the relationships of otherwise puzzling forms. Hennig (1941) investigated it in the Diptera Pupipara, concluding that the slit occurs in at least some genera of the Streblidae, Nycteribiidae

and Hippoboscidae and that all three families are therefore modified Calyptrata. According to him, whenever present the position of the slit marks the true dorsal surface of the second antennal segment, regardless of its shape. The occurrence of the slit has actually been investigated in only a few hippoboscid genera. Jobling (1926) describes and figures the *antennal furrow (AF)* for *Pseudolynchia canariensis* (= *L. maura*), where it is well developed and extends to mid-length of the segment along the dorsal side of the appendage (Fig. 11F). He found it also in *Hippobosca*, but states that it is lacking in *Melophagus*. Hennig (1941) regards it as a primitive characteristic of the Hippoboscidae and explains its absence in certain genera as the result of closing up following the progressively stronger sclerosis of the integument.

Jobling (1926) points out that the hippoboscid antenna is greatly modified no doubt as a sequel to permanent ectoparasitism. He considers that the modifications serve to protect the most important parts of the antenna, namely the third segment and its arista, when the flies move amidst the feathers or hairs of the host. The protection is ensured by the deep antennal pits and the retraction of the third segment within the second. The bristly appendage of the second segment, which occurs in the genera with partly open antennal pit or pits, may also shield the arista from contact with the feathers or hairs. As the main function of the third segment and arista is believed to be olfactory, I suggest, in addition, that the protection is mainly against the exudates and particles of epidermis and dirt which often gather on the surface of the host's skin. Such extraneous matter might easily clog up the openings of the olfactory receptors when the fly feeds. I suggest furthermore that the remarkable development and hairiness of the second segment do not merely protect the third segment, but that they also have an active function. The second antennal segment of insects is known to contain the peculiar organ of Johnston, apparently an important tactile sense organ, registering movements of the distal part of the antenna. In most Hippoboscidae it is eminently suited for this purpose, its surface being enlarged, produced forward and beset with many long and short tactile setae. In the dark recesses of a bird's feathers or a mammal's hairs a fly must rely mainly on the tactile sense to direct its movements. In comparison the sense of smell may be relegated to second place in the life of the fly, accounting for the great reduction of the third antennal segment.

The mouth-parts (Fig. 7A-C; after Jobling) are modified into an extremely efficient piercing and sucking proboscis, which, how-

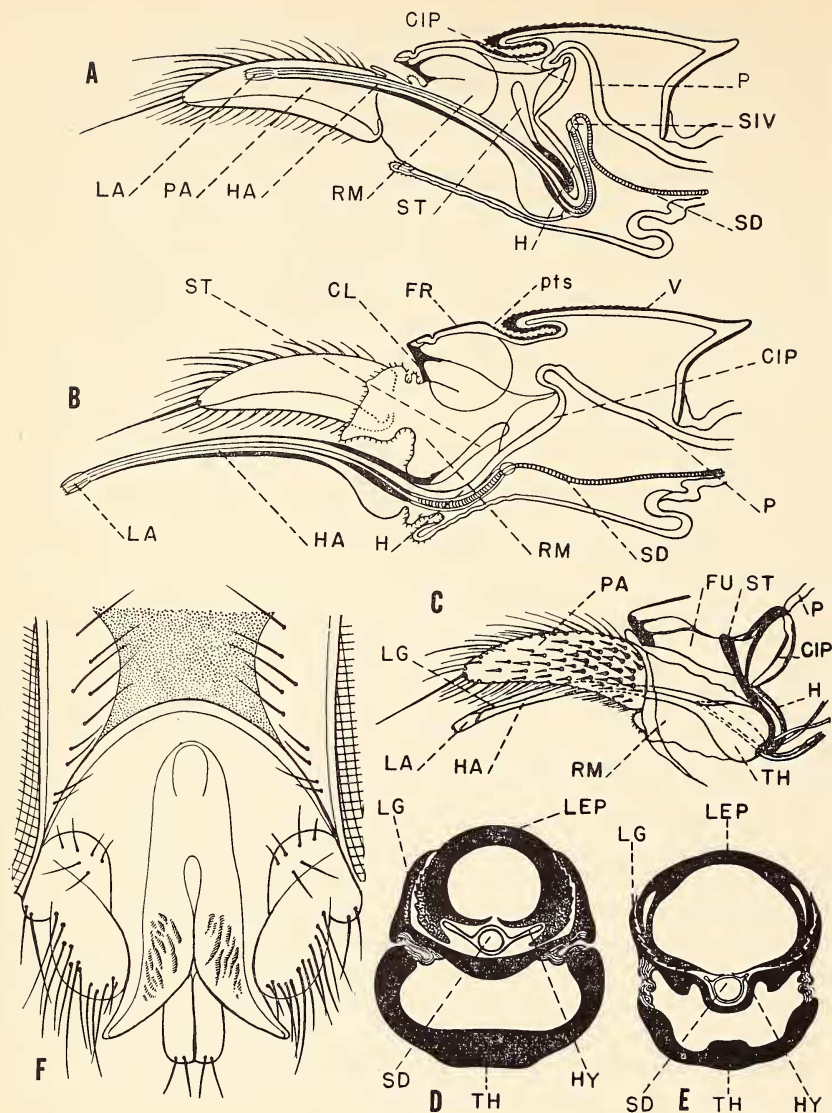


FIG. 7. **A-D**, *Pseudolynchia canariensis* (Macquart); mouth-parts and adjoining structures, modified after Jobling (1926): **A**, longitudinal section with retracted proboscis; **B**, the same with fully extended proboscis; **C**, cleared preparation with proboscis partly everted; **D**, cross-section through middle part of haustellum: CIP, cibarial pump; CL, clypeus; FR, frons; FU, fulcrum; H, hyoid; HA, haustellum; HY, hypopharynx; LA, labella; LEP, labrum-

ever, is duplicated elsewhere in the Diptera, though not exactly in the same manner. The soft basal rostrum membrane (*RM*; basiproboscis), which may be invaginated within the head capsule, bears the several sclerites of the tentorium, called by Jobling the *fulcrum* (*FU*), the *hyoid* (*H*), and the *stipites* (*ST*). The presence of a hyoid (Frey's theca), a small sclerite connecting the fulcrum with the base of the labium (praementum), is considered by Frey (1921, p. 208) a decisive character of calyptrate Muscoidea, which he calls therefore the Thecostomata. The Muscoidea Acalyptrata generally lack a hyoid, for which reason Frey calls them the Haplostomata or Athecostomata. It is somewhat open to question, however, whether the mere presence or absence of a hyoid has such a fundamental importance. Jobling regards its presence as an adaptive feature, correlated with the protractility of the proboscis. The matter is discussed at some length by Hennig (1941, p. 239). In any case, the hyoid is present in the Hippoboscidae, while, according to Jobling, it is present in the Nycteribiidae and absent in the Streblidae. On the sclerites of the tentorium are inserted the muscles of the rostrum which protract and retract the proboscis.

The two single-jointed *palpi* (*PA*; probably the maxillary palpi) protrude from the rostrum beyond the anterior margin of the head. They are almost always well developed and compressed, with concave inner surface, their chief function being to form a protecting sheath around the haustellum. As they usually bear prominent sensorial setae, they have no doubt also a tactile or chemoreceptive function. They are, however, very short and possibly functionless in *Allobosca*, of Malagasy lemurs, and vestigial in *Echestypus*, of African antelopes.

The *haustellum* (*HA*), or sucking tube of the proboscis, is long and narrow, strongly sclerotized. At rest its needle-like distal part lies concealed in the palpal sheath; its bulbous, slightly ovoid base may be protracted or retracted, being withdrawn far within the rostrum membrane and the head capsule when the proboscis is not in use. The haustellum consists of the modified *labium* (*LAB*), which encloses the *labrum-epipharynx* (*LEP*) and the *hypopharynx* (*HY*). These three parts are closely joined (Fig. 7D) and enter the skin as a unit, when the fly bites. The labium ends in two

epipharynx; *LG*, labial gutter; *P*, pharynx; *PA*, palpus; *pts*, ptilinal suture; *RM*, rostrum membrane; *SD*, salivary duct; *SIV*, salivary valve; *ST*, stipes; *TH*, theca; *V*, vertex. **E**, *Glossina palpalis* (Robineau-Desvoidy); cross-section through middle of narrow part of haustellum, modified after Jobling (1933); lettering as in Fig. 7D. **F**, *Olfersia coriacea* Macquart, female; frontal area and antennae.

labella (*LA*; possibly modified labial palpi), provided at the tip with a double crown of *prestomal teeth* (*PRT*; Figs. 6A-B), which act as the cutting organs when the proboscis bores in the skin. According to Frey (1921) and Hennig (1941), true prestomal teeth are also characteristic of the Muscoidea Calyptrata. In all Hippoboscidae the labella are very short as compared with the remainder of the haustellum. The labium is divided over its entire length into two parts, a ventral *theca* (*TH*) and a dorsal *labial gutter* (*LG*), as shown externally by a distinct furrow running on each side along the needle-like part of the labium. The two side walls of the labial gutter are curved upward over the labrum-epipharynx which they enclose more or less completely. The labrum-epipharynx is stylet-shaped, with sharp point, and is a nearly closed tube, with a longitudinal lower (or inner) slit obliterated by the adjacent hypopharynx, thus forming a complete suctorial tube. The outer lateral walls of the labrum-epipharynx are covered with minute teeth, which interlock with similar teeth on the inner walls of the labial gutter (Fig. 7D). The hypopharynx is very slender, but somewhat flattened. Its median, thicker portion is perforated over the entire length by the *salivary duct* (*SD*), which opens in the labial gutter on the dorsal side of the hypopharynx at its narrow distal end. The structure of the proboscis and palpi shows relatively little variation within the family, except in the size of the parts and in minor details. These organs may therefore be regarded as inherited without much change from a common ancestral stock, before the family began to break up into a number of subsidiary groups or sub-families.

The structure of the mouth-parts is the same in both sexes of the Hippoboscidae, as both suck blood. This is true also of the other Pupipara, the Glossinidae and the non-pupiparous blood-sucking Muscoidea.

The foregoing description of the head capsule and mouth-parts follows in the main Jobling (1926), who reviewed, corrected and completed the earlier work of Dufour (1825; 1844; 1845), Muggen-burg (1892), Massonat (1909), Roberts (1927), and others. Jobling studied mainly *Pseudolynchia canariensis* (= *Lynchia maura*) and *Melophagus ovinus*. Gouin (1949, pp. 244-248) recently examined again *Hippobosca equina* and *Melophagus ovinus*. As mentioned before, the area which Jobling had called "fronto-clypeus" (a terminology adopted in my former papers) is not a composite region, as he thought, but represents the frons only (Figs. 6E-F). As in the Muscoidea, the true *clypeus* (*CL*) is the very small sclero-

tized area between frons and rostrum membrane, which Jobling formerly called the tormæ. (See also Snodgrass, 1935, p. 322; and 1943, pp. 36-38 and p. 46, fig. 171).

The depressed *thorax*, more than any other single feature, gives the Hippoboscidae their characteristic louse-like or tick-like appearance. In side view it is often only one-third as high (or thick) as the width of the mesonotum, in contrast to the higher Muscoidea, where it is at least as high as the mesonotal width. In the process of flattening, the sides of the thorax have folded outwardly at two levels, the intervening area of the mesopleura being flat or even concave. The upper or dorsal fold, at about the level of the wing and more or less horizontal, is the stronger and forms a rounded edge or blunt ridge. The lower or ventral fold, at about the upper level of the fore and mid coxae and apparently near the position of the anepisternal suture (*as*) of other Diptera, is often very weak and usually slanting. As a result of the upper fold, the dorsal, horizontal surface of the thorax comprises, in addition to the true notum, the upper portion of the mesopleurites, which in the higher Muscoidea occupy the vertical sides, while the prothoracic spiracles are placed more dorsally. The sternal area also is deeply altered by the flattening. In the higher Muscoidea (Fig. 9B), the sternum and particularly the mesosternum are relatively unimportant, the coxae of each pair being inserted close together, while the legs are strictly ventral. In the Hippoboscidae (Fig. 9A), the sternum is very extensive and the coxae of each pair are widely separated, so that the legs are placed ventro-laterally, allowing them to stretch out and move in a near-horizontal plane. To further complicate matters, some of the sutural lines commonly used as landmarks, but already greatly modified in the higher Muscoidea, have become obliterated. To trace homologies under such conditions is fraught with hazards and may be sometimes pure guesswork.

Dorsally (Fig. 8A) the *pronotum* has a very short median sclerite, or *protergum* (*PT*), usually hidden by the occipital margin. In some cases the *pro-mesonotal suture* (*pms*) is very superficial or obsolete. In the Ornithoicinae and Hippoboscinae (Fig. 11E), the protergum is short, but dorsally visible between head and mesoscutum. Laterally the *propleuron* (*PP*), on which the fore coxa articulates, is sometimes partly visible from above, when the head is free from the thorax; more often it is covered by the projecting angle of the *humeral callosity* (*HC*; humerus or postpronotum). This callosity is as a rule separated, at least partly, from the prescutum by the *posthumeral suture* (*phs*) and bears posteriorly the

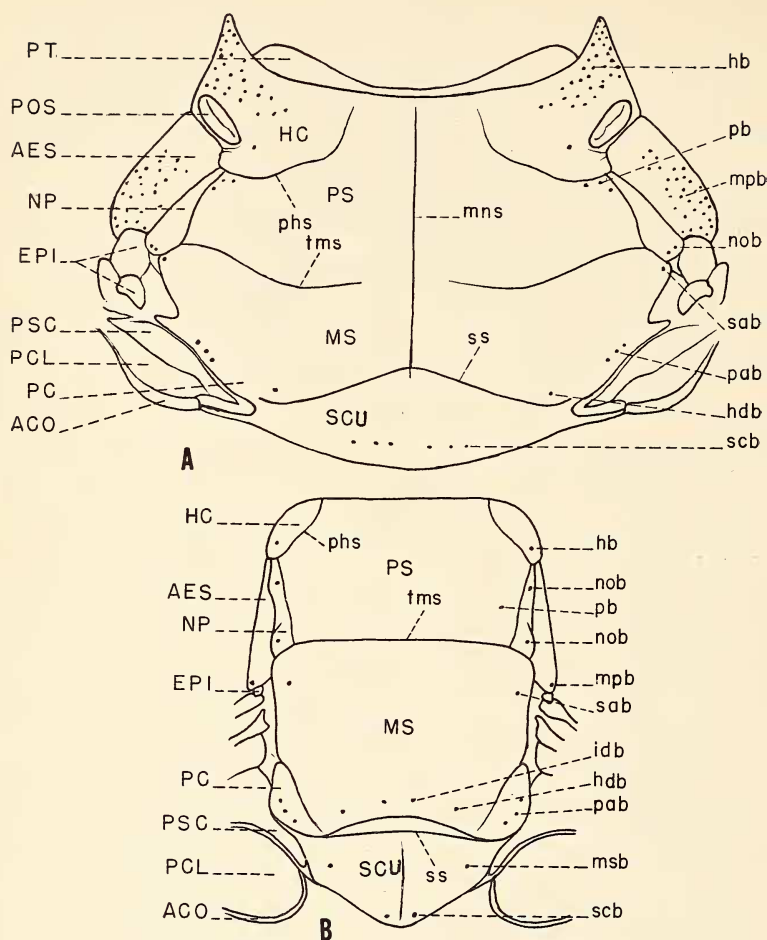


FIG. 8. **A**, *Ornithoetona erythrocephala* (Leach), female; thorax from above. **B**, *Glossina fusca* Walker, female; thorax from above. ACO, axillary cord; AES, anepisternum; EPI, epipleurite; hb, humeral bristles; HC, humeral callosity; hdb, posterior dorso-central bristle; idb, posterior acrostichal bristle; mns, medium notal suture; mpb, mesopleural bristles; MS, mesoscutum; msb, discoseutellar bristle; nob, notopleural bristles; NP, notopleuron; pab, postalar bristles; pb, presutural bristles; PC, postalar callus; PCL, lower calypter; phs, posthumeral suture; POS, prothoracic spiracle; PS, prescutum; PSC, paraseutellum; PT, protergum; sab, supraalar bristle; scb, scutellar bristles; SCU, scutellum; ss, scutoseutellar suture; tms, transverse mesonotal suture.

conspicuous, more or less dorsally placed *prothoracic spiracle* (*POS*). Whether the humeral callosity includes in addition some other propleural sclerite (episternum or epimeron) is open to question.

The *mesonotum* occupies the major part of the dorsum. In *Ornithoica*, *Ornithomyia*, and *Ornithoctona* (Fig. 8A), where it is most similar to that of the Muscoidea, it is divided behind mid-length by a straight, *transverse mesonotal suture* (*tms*), often somewhat interrupted medially, into an anterior *prescutum* (*PS*) and a posterior *mesoscutum* (*MS*). It may also show a longitudinal superficial *median notal suture* (*mns*), running from the anterior margin to close to the scutellum. A narrow, wedge-shaped *notopleuron* (*NP*), on each side before the mesonotal suture, is set off by deep grooves from the prescutum and mesopleuron. In other genera the mesonotal suture undergoes various changes or disappears. In *Lipoptena* (Fig. 11A), the median notal suture is indicated only anteriorly; instead the mesonotum bears a pair of superficial longitudinal *intrascutal grooves* (*lig*). Likewise the notopleuron may be partly or completely fused with the prescutum, its position being then indicated only by the insertion of the *notopleural bristles* (*nob*; posthumeral bristles); in *Hippobosca* (Fig. 11E), *Lynchia*, and *Olfersia* the fusion is complete; it is as yet incomplete in some species of *Lipoptena* (Fig. 11A) and *Stilbometopa*. *Postalar calli* (*PC*) are rarely or only superficially set off at the outer hind corners of the mesoscutum, although *postalar bristles* (*pab*) are often present. The large dorsal sclerite, on each side between the prothoracic spiracle and the base of the wing, is the upper portion of the mesopleuron, or *anepisternum* (*AES*), which has moved to a horizontal position. My former interpretation of this sclerite in *Lipoptena* as the notopleuron (1942a, p. 9 and fig. 1E, *NP*) was erroneous and is corrected in Fig. 11A. The stiff setae near its hind margin or scattered over the surface, correspond to the upper *mesopleural bristles* (*mpb*) of the Muscoidea. The two small sclerites often found between the hind margin of the anepisternum and the root of the wing, may be modified *epipleurites* (*EPI*). Exceptionally, as in *Melophagus*, all mesonotal sutures are nearly obliterated.

The *scutellum* (*SCU*), often large, is limited anteriorly by a *scuto-scutellar suture* (*ss*), usually deep and complete. In *Melophagus*, where the scutellum is small, it is nevertheless set off by a shallow suture. It generally shows a longitudinal depression, sometimes widened triangularly. Laterally it continues in an ante-

rior and a posterior ridge, enclosing on each side a more or less grooved area, the *parascutellum* (*PSC*). In most Hippoboscidae the anterior ridge is little developed or is fused with the hind margin of the postalar callus; it is well defined in *Ornithoica*. The *postscutellum* (*POU*; postnotum), lies behind and below the scutellum from which it is rarely separated by a narrow *subscutellum* (*SSL*) in the Hippoboscidae; but its two lateral areas, the *pleurotergites* (*PTG*) of the metanotum, are sometimes much swollen or bear characteristic *pleurotergal processes*. Below the postscutellum lies the *metanotum* (*MTN*), usually developed on the sides only or fused with one of the adjoining sclerites.

The reduction of the sternal area in most Diptera, particularly pronounced in the calyptrate Muscoidea, and the resulting near-contiguity of the coxae in each pair are the extreme development of a peculiarity common to all Neuropteroidea. In these insects part or most of the primitive or true sternum, with the paired internal sternal apophyses, are inflected on the middle line by so-called cryptosterny, producing a forked endoskeletal apodeme, the *furca*, usually traced outwardly as a median sternal or *furcal suture* (*fu1*, *fu2*, *fu3*). In the more primitive winged insect thorax, the bases of the sternal apophyses are often connected by an internal sternocosta, forming externally a sternocostal suture which divides the sternum proper into a presutural *basisternum* (*BS1*, *BS2*, *BS3*) and a postsutural *furcasternum* (*FS1*, *FS2*, *FS3*; sternellum); anterior to the basisternum, an additional small median sclerite, the *presternum* (*PS1*, *PS2*, *PS3*), is sometimes detached. In the Diptera, however, these several areas have undergone many shifts; some of the original sutures have disappeared and new ones have secondarily taken their place, so that it is extremely difficult and perhaps even impossible to trace the true sternal homologies. This will be realized from a comparative study of the sternum of *Glossina fusca* (my Fig. 9B), *Calliphora* (Snodgrass 1935, p. 171, fig. 95B), and *Musca* (Hennig, 1941, pl. 9, figs. 1-2). In all these figures a partly developed longitudinal suture runs forward on each side from the insertion of the mid coxae (weakest in *Musca*). This may possibly be a remnant of the original division between the sternum and the pleura or laterotergites. It should also be noted that the mid coxae are more widely separated from each other in *Glossina* than in either *Musca* or *Calliphora*, no doubt owing to the slight flattening of the thorax of the tsetse-fly.

Neither Snodgrass (1935) nor Crampton (1942) attempt to trace the homologies of the sternal regions of the Diptera. Cramp-

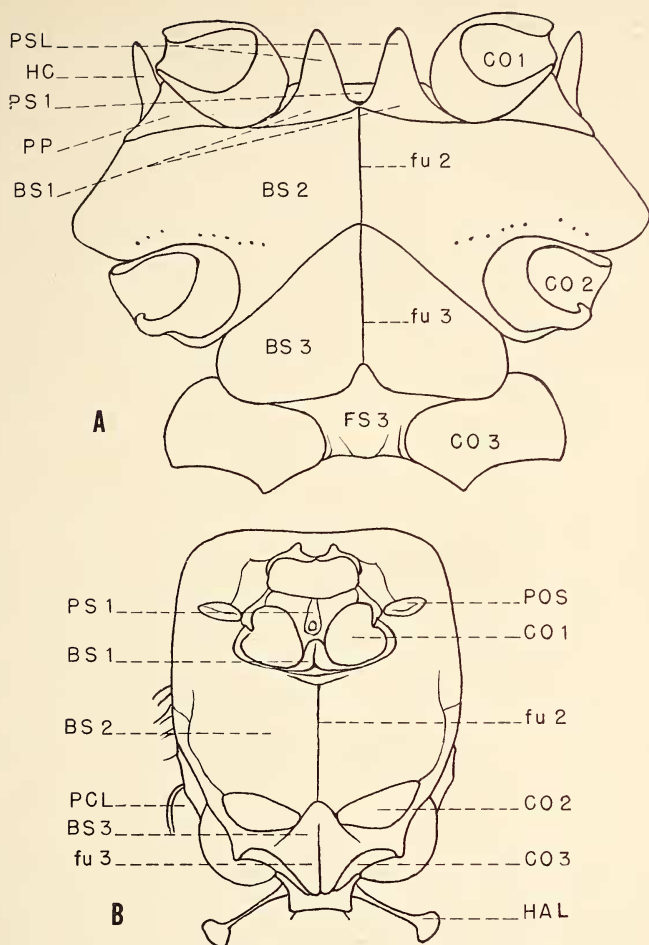


FIG. 9. **A**, *Ornithoetona erythrocephala* (Leach), female; thorax from below. **B**, *Glossina fusca* Walker, female; thorax from below. *BS1*, basisternum of prothorax; *BS2*, basisternum of mesothorax; *BS3*, basisternum of metathorax; *CO1*, *CO2*, *CO3*, fore, mid and hind coxae; *FS3*, furcasternum of metathorax; *fu2*, furcal suture of mesosternum; *fu3*, furcal suture of metasternum; *HAL*, halteres; *HC*, humeral callosity; *PCL*, lower calypter; *PP*, propleuron; *PS1*, presternum of prothorax; *PSL*, prosternal lobes.

ton merely labels each of the three sternal divisions of *Ornithoctona* as basisternum (*bs*) on a side view of the thorax (1942, fig. 6E). He also distinguishes as furcasternum (*fs*) a posterior area of the prosternum; I am unable to find a suture separating such a region in *Ornithoctona erythrocephala*. The only study of the hippoboscoid sternum now available is that by Hennig (1941). His suggestions as to the internal changes involved in dipterous cryptosterny and their relations to the later, secondary widening of the sternum in the Pupipara deserve serious consideration. He does not, however, propose a terminology that might be used for the several areas, some of which are of great importance for the taxonomy of these flies. It is rather unfortunate that he selected *Hippobosca* for his study, as this is one of the more specialized of the Hippoboscidae.

The thorax of the Ornithoicinae (*Ornithoica*), the most primitive of the Recent Hippoboscidae, is less depressed than that of the other subfamilies, and the three main divisions are more clearly defined. On the sternum seen from below (Fig. 12B), some of the pleural areas are visible on each side, and, in the mesothorax, the lower portion of the *anepisternum* (*AES*) is separated from the sternum proper by a slight depression, but without any real suture. The *prosternum* consists of a single, moderately wide, trapezoidal, intercoxal *basisternum* (*BS1*), without longitudinal depression; in front of it the cervical membrane has no additional sclerite. The *mesosternum* comprises a single sclerite, presumably the combined *basisternum* (*BS2*) and *furcasternum* (*FS2*), the lateral portions of the latter being set off as triangular areas in the hind corners near the mid coxae by very weak transverse depressions (without suture); a median *furcal suture* (*fu2*) runs the whole length of the mesosternum. Young (1922) regards the area here called the mesosternum as corresponding to the lower portions of the episterna (sternopleura), which may have crowded out the true basisternum and furcasternum. This view may be morphologically correct and would fall in line with Hennig's (1941) contention that, when the coxae of the Hippoboscidae moved apart, they merely shifted laterally, presumably within the pleural sclerites, all the true sternal areas having become permanently absorbed in the endoskeletal furca. The *metasternum* consists of two sclerites: the anterior, larger area, or *basisternum* (*BS3*), is divided throughout by a deep median *furcal suture* (*fu3*); the posterior, very small portion, or *furcasternum* (*FS3*), is undivided.

The sternum of the other Hippoboscidae fits in the same general pattern, as a comparison with *Ornithoctona* (Fig. 9A), *Hippobosca*

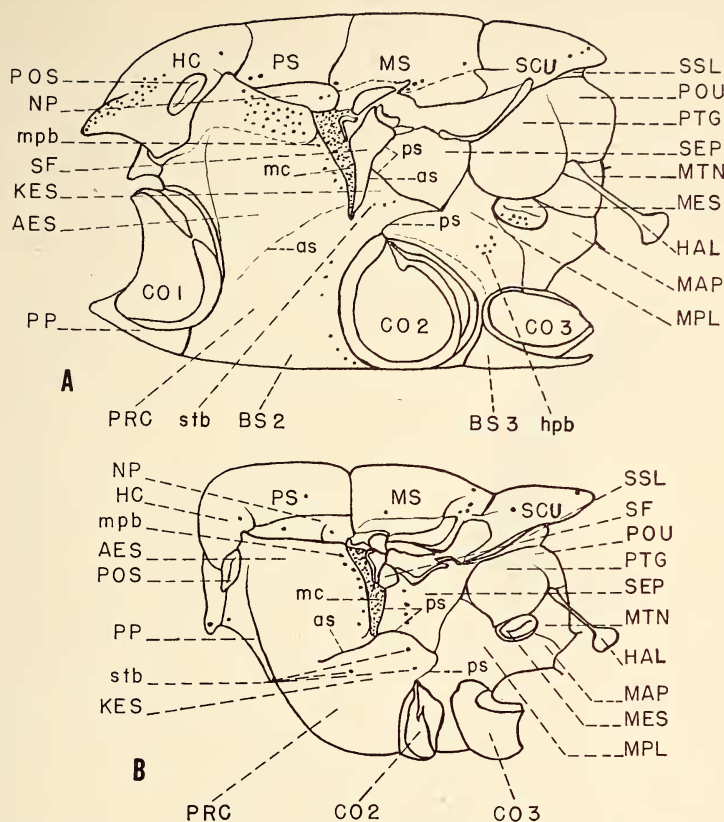


FIG. 10. **A**, *Ornithoetona erythrocephala* (Leach), female; thorax in side view. **B**, *Glossina fusca* Walker, female; thorax in side view. AES, anepisternum; as, anepisternal suture; BS2, basisternum of mesothorax; BS3, basisternum of metathorax; CO1, CO2, CO3, fore, mid and hind coxae; HAL, halteres; HC, humeral callosity; hpb, hypopleural bristles; KES, katapisternum; MAP, metapleuron; mc, membranous cleft of pleuron; MES, metathoracic spiracle; mpb, mesopleural bristles; MPL, meropleurite; MS, mesoscutum; MTN, metanotum; NP, notopleuron; POS, prothoracic spiracle; POU, post-scutellum; PP, propleuron; PRC, precoxal area; ps, pleural suture; PS, pre-scutum; PTG, pleurotergite; SCU, scutellum; SEP, supraepimeron; SF, subalifer; SSL, subscutellum; stb, sternopleural bristles.

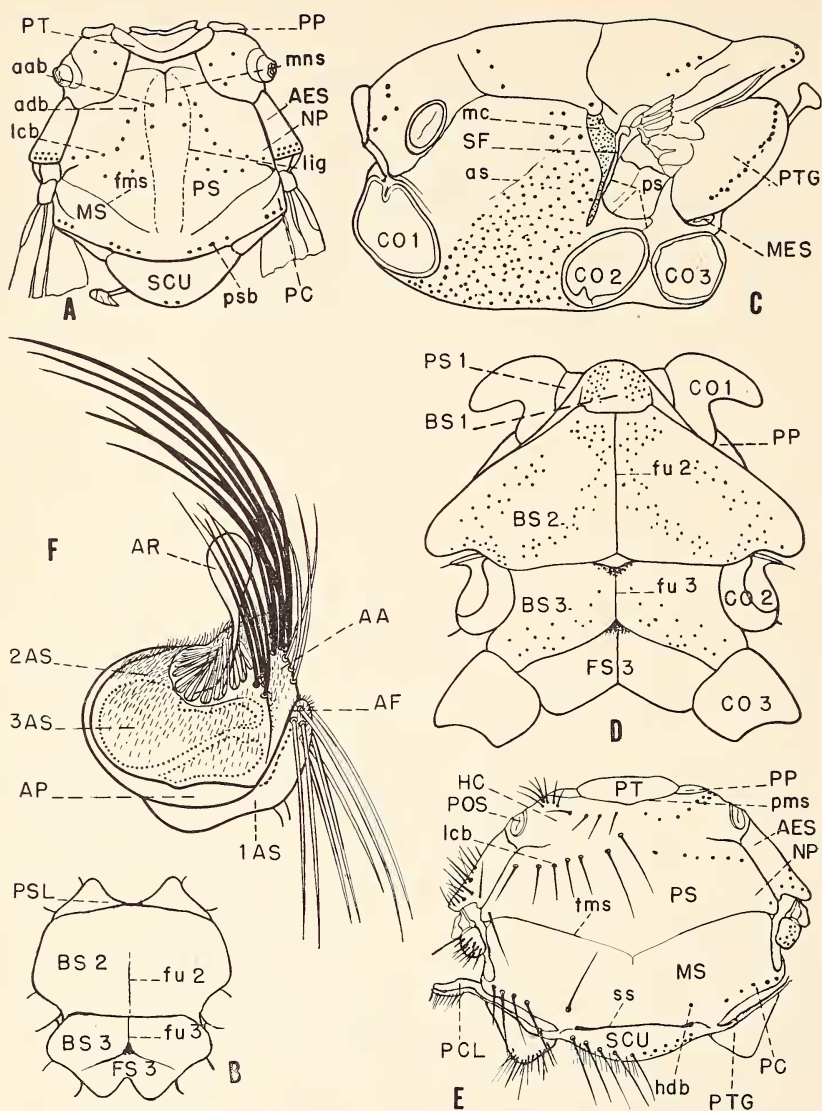


FIG. 11. **A-B**, *Lipoptena depressa* (Say), female; thorax from above (**A**) and below (**B**): aab, anterior acrostichal bristle; adb, anterior dorso-central bristle; AES, anepisternum; BS2, basisternum of mesothorax; BS3, basisternum of metathorax; FS3, furcasternum of metathorax; fu2, furcal suture of mesothorax; fu3, furcal suture of metathorax; lcb, latero-central bristles; lig, longitudinal intraseutal groove; mns, median notal suture; MS, mesoscutum;

(Fig. 11D), *Lipoptena* (Fig. 11B), and *Melophagus* will show; the mesosternum extends farther to the sides, thus hiding the pleural areas. The prosternum and metasternum also widen and there are various other minor changes. In *Lipoptena* and *Melophagus*, the prosternum is deeply emarginate anteriorly; in *Ornithomyiinae*, it is divided into a pair of lobes or prongs, the *prosternal lobes* (*PSL*), directed forward. *Hippobosca* is peculiar in that the hind lateral areas of the mesosternum (sides of the furcasternum) are separated from it by a suture and fused with the basisternum of the metathorax.

The *pleura* of the Hippoboscidae are best understood by comparing them with those of the higher Muscoidea, in which they are moreover already greatly modified from those of more primitive winged insects. The following areas may be recognized in *Glossina fusca* (Fig. 10B). The *propleuron* (*PP*) is very short and incompletely divided from the mesopleuron. In the more primitive winged insects, a pleural suture runs a fairly simple, oblique course from the pleural wing process to the pleural coxal process and divides the *mesopleuron* into an anterior *episternum* and a posterior *epimeron*. In the Muscoidea, however, the *pleural suture* (*ps*) follows a zigzag course, with two angular bends, dividing it into three sections: the first (anterior) bend sends forth a slightly slanting *anepisternal suture* (*as*), which divides the *mesepisternum* into an anterior (upper) *anepisternum* (*AES*) and a posterior (lower) *katepisternum* (*KES*), the latter fused with the lower *precoral area* (*PRC*); at the second (posterior) bend, an upward running suture divides the *mesepimeron* also into an anterior (upper) *supraepimeron* (*SEP*; anepimeron) and a posterior (lower) *infraepimeron*, the latter fused with the meron of the mid coxa to form a *meropleurite* (*MPL*). A vertical *membranous cleft* (*mc*), in front of the upper section of the pleural suture, extends as far

NP, notopleuron; *PC*, postalar callus; *PP*, propleuron; *PS*, prescutum; *psb*, prescutellar bristles; *PSL*, prosternal lobes; *PT*, protergum; *SCU*, scutellum; *tms*, transverse mesonotal suture. **C-E**, *Hippobosca equina* Linnaeus, female; thorax in profile (**C**), from below (**D**) and from above (**E**): *as*, anepisternal suture; *BS1*, basisternum of prothorax; *CO1*, *CO2*, *CO3* fore, mid and hind coxae; *hdb*, posterior dorsocentral bristle; *HC*, humeral callosity; *mc*, membranous cleft of pleuron; *MES*, metathoracic spiracle; *PCL*, lower calypter; *pms*, promesonotal suture; *POS*, prothoracic spiracle; *ps*, pleural suture; *PS1*, presternum of prothorax; *PTG*, pleurotergite; *SF*, subalifer; *ss*, scuto-scutellar suture; other lettering as in Fig. 11A-B. **F**, *Pseudolynchia canariensis* (Macquart); left antenna from the side, after Jobling (1926): *AA*, antennal appendage; *AF*, antennal furrow; *AP*, antennal pit; *AR*, arista of third segment; *1AS*, *2AS*, *3AS*, first, second and (outline of) third antennal segments.

down as the anepisternal suture. Some small sclerites are wedged in the upper corner of this cleft, between the pleural suture and the base of the wing; the most conspicuous of these is the *subalifer* (*SF*). The *metapleuron* (*MAP*), below the metathoracic spiracle (*MES*), is fused anteriorly with the meropleurite. The combined metapleuron, meron of mid coxa and infraepimeron of the mesopleura of the Muscoidea form the area usually called the *hypopleuron* by dipterists and bearing the *hypopleural bristles* (*hpb*). The insertion of the *halter* (*HA*) marks the separation of the *metanotum* (*MTN*) from the pleurotergites of the postscutellum.

In *Ornithoctona erythrocephala* (Fig. 10A), most of the sutures and areas of the pleura of *Glossina* may be recognized, but are somewhat modified. The two bends of the pleural suture are more angular, particularly the lower one; while the anepisternal suture is nearly vertical, extending the first section of the pleural suture downward. The metapleuron appears to be very superficially divided from the meropleurite of the mesopleura. The *subalifer* (*SF*) is greatly developed and wedged in between the membranous cleft and the anepisternal suture. In most other genera of Hippoboscidae, for instance in *Hippobosca* (Fig. 11C), the sclerites of the pleura are more difficult to trace, some of the sutures becoming obsolete, particularly in the subapterous forms. In *Melophagus* nearly all dorsal and lateral sutures of the thorax have disappeared, although a few are retained on the sternum; the dorso-ventral flattening has even affected the metapleura, so that the metathoracic spiracles also are in a dorsal position. It would seem meaningless to trace any homologies of parts or areas in such a highly specialized complex.

The *legs* (Fig. 12C-E) are robust, with rather swollen femora, flattened tibiae and short, compact tarsi. They vary in length and are on the whole shorter and stouter in the mammal-inhabiting forms than in those of birds. In the latter the legs are adapted to gliding and scurrying about swiftly, forward, backward, as well as sideways, amidst the soft feathers; in the former they are built more for grasping and adhering to the skin and to the coarse hair of the pelt. The *coxae* (*CO1*, *CO2* and *CO3*) are large and swollen; those of the fore legs are more or less balloon-shaped and freely movable, so that they may be directed downward as well as sideways; but the mid and hind coxae are flattened, horizontal and sometimes nearly immovable. The *trochanters* (*TR*) of the fore legs are small, as usual in the Diptera; those of the mid and hind legs are larger and movable on both coxa and femur, obviously to

compensate for the relative fixity of their coxae. The *femora* (*FE*) and *tibiae* (*TI*) show no unusual features. The *tibial spurs* (*TSP*) are sometimes difficult to trace amidst the apical bristles. The *tarsi* (*TAR*) consist of five short segments and a terminal *pretarsus* (de Meijere; Ockler's "Krallenglied"). The basal segment or *basitarsus* (*BTA*) of the hind tarsi is sometimes more elongate than the others; the fifth segment or *distitarsus* (*DTA*) is always broad and depressed. The *pretarsus* consists of a membranous, elastic base (Ockler's "abschliessende Haut"), which bears a median, slender, often hairy or feathered *empodium* (*EMP*; Ockler's "Streckborste"; de Meijere's "Sohlenfortsatz" or "Sohlenborste"), flanked on each side by a broad, flap-like *pulvillus* (*PU*; "Haftläppchen" of Ockler) and a *claw* (*UN*; *unguis*; Ockler's "Kralle"). A small, transversely striate, median, sclerotized *unguitractor plate* (*UTR*; Ockler's "Streckplatte") lies in the membranous base on the under side of the pretarsus; attached to its proximal end is the tendon of the retractor muscle of the claws.

In all the Hippoboscidae, of mammals as well as of birds, two claws are present on all legs. They are unusually developed and consist of a broad, flattened base or *heel* (*HE*), followed by one or two teeth (*TO*). The heel has a basal protuberance hinged to the dorsal apical margin of the distitarsus on either side of a median *unguifer process* (*UP*; Ockler's "Krallengelenkhöcker"); its apical portion is prominent and sometimes prolonged, simulating an additional tooth. Simple claws (Fig. 12F), ending in one tooth, occur in all mammal-infesting flies (Hippoboscinae, Melophaginae, Ortholfersiinae, and Alloboscinae) and in the bird-flies of the subfamily Ornithoicinae; their claws are sometimes said to be bidentate or bifid (Meigen, 1830, p. 230; Kieffer, 1900, p. 338), owing to the greatly developed, tooth-like basal heel, which is strongly sclerotized and darkened along the inner edge. The remaining bird-flies (Ornithomyiinae) have claws with two separate teeth, in addition to the basal heel (Fig. 12K); as the basal heel is even more elongate than that of the simple claws, the claws of the Ornithomyiinae are sometimes called by error tridentate or trifid (Kieffer, 1900). Actually, the additional tooth is due to the cleaving of the basal heel; in some of the flies with simple claws the basal heel shows a deep longitudinal groove. The claws are mobile and each of them can move independently in a pair.

The pulvilli of the Hippoboscidae also differ markedly from those of other Diptera. As Ockler (1890, pp. 33 and 36) pointed out, they show peculiar adaptations to ectoparasitic life amidst fur

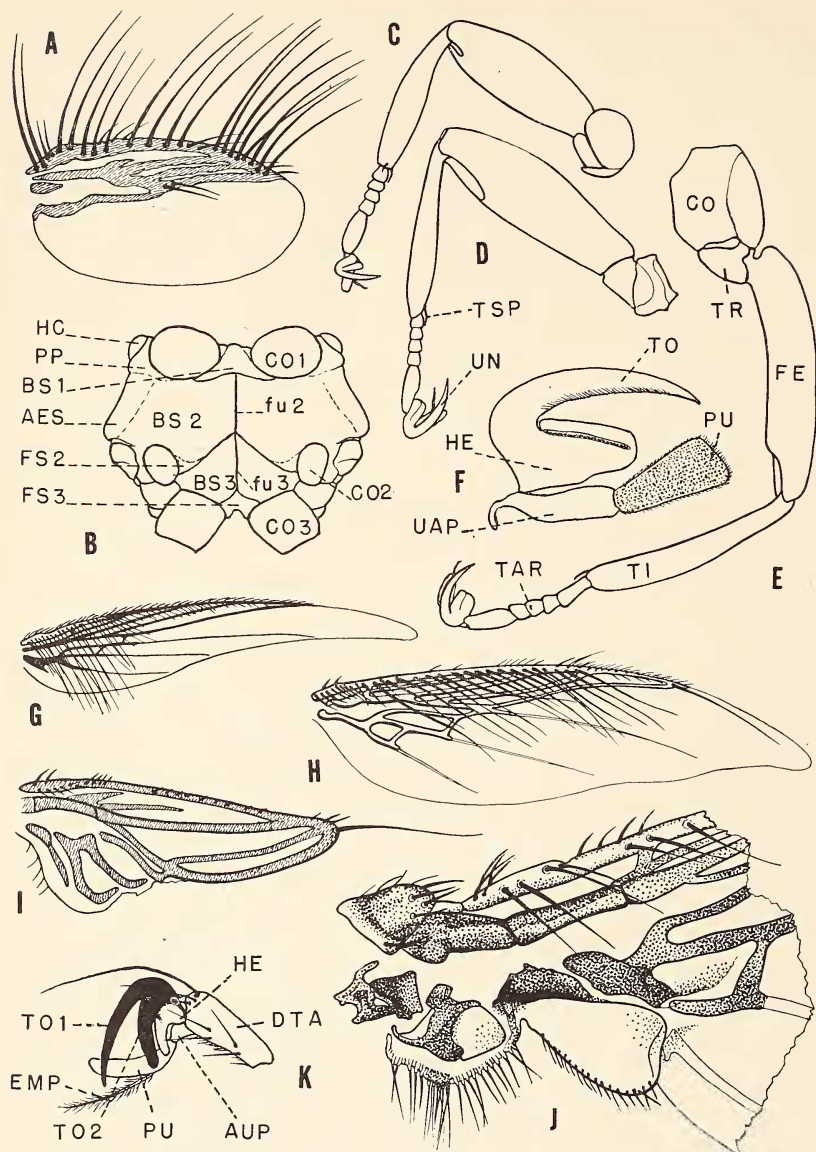


FIG. 12. **A**, *Myiophthiria lygaeoides* Rondani, female; wing. **B**, *Ornithoica vicina* (Walker), female; thorax from below: *AES*, anepisternum; *BS1*, *BS2*, *BS3*, basisternum of pro-, meso-, and metathorax; *CO1*, *CO2*, *CO3*, fore, mid and hind coxae; *FS2*, *FS3*, furcasternum of meso- and metathorax; *fu2*, *fu3*, furcal suture of meso- and metasternum; *HC*, humeral callosity; *PP*, propleura. **C-F**, *Hippobosca equina* Linnaeus, female; **C-E**, fore, mid and hind legs: *CO*,

and plumage. The fully-extended pulvillus is a lengthened, tender and soft flap inserted on a long, narrow, sclerotized *auxiliary plate* (*AUP*; Ockler's "Stützplatte") attached to the membranous base of the pretarsus. When the pulvilli function they are projected forward between the claws, which simultaneously are raised and spread out, their bases being thrown back over the dorsal apex of the distitarsus. The claws are lowered when in use and at the same time the pulvilli are folded back beneath the apical area of the distitarsus where they lie spread out flat, side by side, and are protected by the prominent, broad apical portion of the heels of the claws.

In some, but not in all louse-flies of mammals, the pretarsus is asymmetrical, the claws being unequal in each pair, one being thicker or shorter (J. Bequaert, 1942a, p. 68; fig. 5E, inner and outer claw of fore leg of *Lipoptena cervi*). The unequal claws were first described by Meigen (1830, p. 230) for *Lipoptena cervi* (= *Ornithobia pallida*). In most hippoboscids with unequal claws the pulvilli also are unequal in each pair, as de Meijere (1901, pp. 446 and 467) noted for *Lipoptena cervi*, where the larger pulvillus adjoins the shorter claw. This is true also in most species of *Hippobosca* (such as *H. equina*); in others one of the pulvilli is rudimentary. *Hippobosca camelina* is unique in the genus in that the very long claws are equal in each pair, while both pulvilli are completely aborted.

The *wings* vary in size and shape. In the majority of the genera (15 out of 20) and species (107 out of 124), they are well developed and functional, being relatively long and broad for the size of the body. Such fully-winged flies occur on birds as well as on mammals, and both types of hosts also harbor species with more or less reduced wings, no longer used for flight. The normally subapterous forms belong to 4 genera, with some 15 species. *Melophagus*, containing two species on mammals, is the only genus with completely atrophied wings, reduced to minute, elongate, setigerous knobs. In 3 of the winged genera, with 18 species on mammals, related to *Melophagus*, the newly emerged fly has fully-developed and func-

coxa; *FE*, femur; *TAR*, tarsus; *TI*, tibia; *TR*, trochanter; *TSP*, tibial spur; *UN*, claw; *F*, smaller claw and adjoining pulvillus of fore leg; *UAP*, auxiliary plate; *HE*, heel; *PU*, pulvillus; *TO*, tooth. **G**, *Stenopteryx hirundinis* (Linnaeus), female; wing. **H**, *Crataerina pallida* (Latreille), female; wing. **I**, *Allobosca crassipes* Speiser, female; wing. **J**, *Ornithoeza metallica* (Schiner), female; base of wing. **K**, *Ornithomyia fringillina* Curtis, female; distitarsus and pretarsus: *AUP*, auxiliary plate; *DTA*, distitarsus; *EMP*, empodium; *HE*, heel of claw; *PU*, pulvillus; *TO1*, *TO2*, double teeth of claw.

tional wings, which break off close to the base after the final host is reached.

When it is most complete, as in *Ornithoetona* and *Ornithomyia* (Fig. 13A), the venation is similar to that of the Myiodaria Calyptrata, except for two minor peculiarities. The normal muscoid venation is itself greatly reduced, as compared to that of the lower Nematocera. The resulting difficulty in tracing the homologies of the veins is particularly felt in the Hippoboscidae, and is even enhanced in *Lipoptena*, *Neolipoptena*, and *Echestypus*, which show the greatest reduction of veins in a fully-developed wing of any of the Cyclorrhapha. For descriptive purposes I prefer to a so-called morphological terminology one of the purely conventional terminologies of veins and cells of the older authors. I find this less confusing than the now popular notations derived from the Comstock-Needham system, based on the real or supposed homologies of the dipterous venation with that of other insect orders. Comstock applied his notations in their present form to a hippoboscid for the first time in 1924 (p. 874, fig. 1118, labelled *Olfersia* sp.; actually of a *Lynchia*, presumably *L. americana*). Soon afterward, Tillyard (1926, p. 378, fig. W73) offered a modification shown for the wing of an Australian species of *Ornithomyia* which he called *O. australasiae*, but which was probably not Fabricius' species of that name. In this, the 4th longitudinal became M_1 (instead of M_{1+2}), the 5th longitudinal $M_3 + Cu_1$ (instead of M_{3+4}), and the 6th longitudinal $Cu_1 + 1An$ (instead of *1st A*). Ferris and Cole (1922, p. 196) stated that their interpretation was in accord with the Comstock-Needham system, presumably as first published with a different type of notations by J. H. and A. B. Comstock in 1895 (p. 488, fig. 595); but Comstock's vein *1st A* becomes Cu_2 in their fig. 12 supposedly of *Lynchia americana* (more probably *L. fusca* of California) and *2nd A + Cu₂* in their fig. 18 of *Stilbometopa impressa*, where in addition the cross-vein closing the anal cell is labelled as part of Cu_2 . In 1925 (p. 418, fig. 4) Ferris used again $Cu_2 + 2nd A$ in the wing of *Ornithoeza metallica* for Comstock's *1st A*, while the axillary vein behind it is labelled *3rd A* (instead of *2nd A*). More involved changes of the Comstock notations were proposed recently by Lower (1951, p. 81, fig. 22, wing of *Ornithomyia* sp.). It would seem pointless to discuss more in detail the several emendations of the Comstock system proposed in this country and abroad, since my remarks are not intended as criticism, but merely show the lack of agreement in the matter. Nevertheless, I have inserted in the following list of terms the

equivalent notations of the original Comstock system and some of the suggested changes, so that the reader may use them, if he wishes.

Costa (*CO* in Fig. 13A; *C* of Comstock), strongly developed along the anterior margin and ending at the tip of the 3rd longitudinal vein or slightly beyond it. The apical and posterior margins never show a trace of an ambient vein. The costa always bears many setae, some often very long, particularly toward the base. A *costal spine* or bristle, at the termination of the subcosta, is rarely present (in *Ornithoica*).

Subcosta (*SC* in Fig. 13A and of Comstock; mediastinal or auxiliary vein), sometimes not continued to the costa. A short *humeral cross-vein* (*h* in Fig. 13A; *h* or *hm* of Comstock; Speiser's "basale Querader"; Townsend's first subcostal vein) connects it with the costa a short distance from the base.

First longitudinal vein (1 in Fig. 13A; R_1 of Comstock; R_{1+2} of Lower, 1951; Speiser's Subcostalis).

Second longitudinal vein (2 in Fig. 13A; R_{2+3} of Comstock, 1924; R_3 of Lower, 1951; radial vein; Speiser's Radialis), sometimes running close to or partly fused with the costa, apically (in *Ornithoica*, Fig. 14D).

Third longitudinal vein (3 in Fig. 13A; R_{4+5} of Comstock, 1924; R_4 of Lower, 1951; cubital vein; Speiser's Cubitalis), sometimes more or less confluent with the costa apically (in *Ornithoica*).

Fourth longitudinal vein (4 in Fig. 13A; M_{1+2} of Comstock, 1924; M_1 of Tillyard, 1926; $R_5 + M_1$ of Lower, 1951; discal vein; Speiser's Discoidalis). This is always connected with the 3rd longitudinal, usually about mid-length in the wing, by means of a short *anterior cross-vein* (*r-m* in Fig. 13A and of Comstock, 1924; r_4-m of Lower, 1951; first basal, median, middle, outer, or small cross-vein; Speiser's "kleine Querader"; Tillyard's radio-median cross-vein; Ferris' radial-medial cross-vein).

Fifth longitudinal vein (5 in Fig. 13A; $M_3 + Cu_1$ of Comstock, 1924; M_{3+4} of Tillyard, 1926, and of Lower, 1951; Speiser's Posticalis). In some genera this is connected, by means of the *anterior basal cross-vein* (M_3 in Fig. 13A and of Comstock, 1924; M_{3+4} of Lower, 1951; basal or inner cross-vein; Speiser's "hintere Querader"), with the 4th longitudinal, basad of the anterior cross-vein.

Sixth longitudinal vein (6 in Fig. 13A; $Cu_1 + 1st A$ of Comstock, 1924; anal vein). In some genera this is connected with the 5th longitudinal by means of the *posterior basal or anal cross-vein* (*ac* in Fig. 13A; given no notation by Comstock, Tillyard and Lower; Cu_2 of Ferris and Cole, 1922; Speiser's "Analquerader").

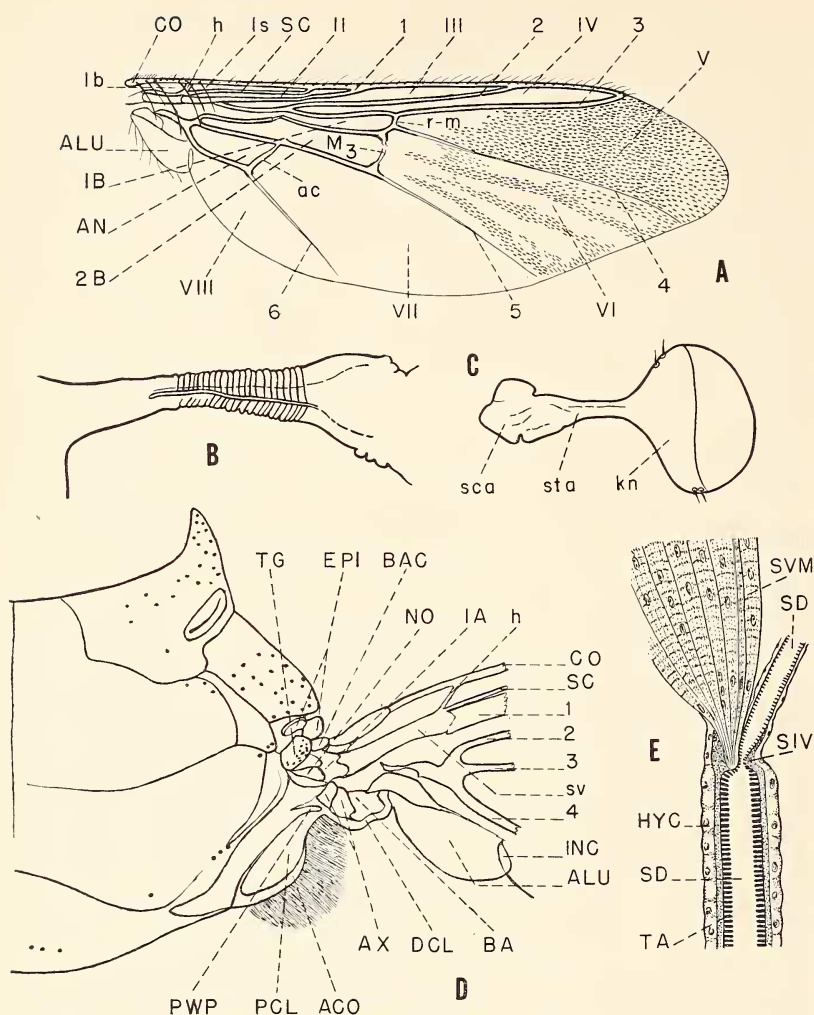


FIG. 13. **A**, *Ornithomyia fringillina* Curtis, female; wing: *ac*, posterior basal cross-vein; *ALU*, alula; *AN*, anal cell; *1B* and *2B*, first and second basal cells; *CO*, costa; *h*, humeral cross-vein; *M₃*, anterior basal cross-vein; *r-m*, anterior cross-vein; *SC*, subcosta; *1*, *2*, *3*, *4*, *5*, and *6*, first, second, third, fourth, fifth and sixth longitudinal veins; *Ib*, basal costal cell; *Is*, second costal cell; *II*, subcostal cell; *III*, marginal cell; *IV*, submarginal cell; *V*, first posterior cell; *VI*, second posterior cell; *VII*, third posterior cell; *VIII*, axillary cell. **B**, *Lipoptena cervi* (Linnaeus); stalk of halter, after Brauns (1939). **C**, *Ornithomyia biloba* Dufour; halter, after Brauns (1939): *kn*, knob; *sca*, scabellum; *sta*, stalk. **D**, *Ornithoctona erythrocephala* (Leach), female; right dorsal half of thorax and base of wing: *ACO*, axillary cord; *ALU*, alula;

Axillary vein (2nd *A* of Comstock), usually absent or vestigial, except at the thickened extreme base.

The 4th, 5th and 6th longitudinals are generally weak and discolored beyond the cross-veins and never reach the hind margin. The veins are usually bare, except the costa; in some species one or more longitudinals may be partly or mostly setulose on the upper side. The anterior basal cross-vein frequently shows a discolored stretch, or *bullæ* (*BU*), which in *Lynchia* and *Olfersia* is so extensive that the vein appears to be obliterated. There may be a similar bulla basally on the 4th longitudinal near the middle of the 2nd basal cell and the vein may be bent upward at this point to run for some distance closer to the base of the 3rd longitudinal. A small bulla is rarely indicated at the upper end of the anal cross-vein. Bullae appear to be absent in most higher Muscoidea; but in *Glossina* there is at least a trace of one in the anterior basal cross-vein.

Costal cell (*I* in Fig. 13A; *C* of Comstock; mediastinal), between costa and subcosta, divided by the humeral cross-vein into a *basal costal* (*Ib* in Fig. 13A) and a *second costal* (*Is* in Fig. 13A).

Subcostal cell (*II* in Fig. 13A; *Sc* of Comstock), between subcosta and 1st longitudinal.

Marginal cell (*III* in Fig. 13A; *R*₁ of Comstock), between 1st and 2nd longitudinals.

Submarginal cell (*IV* in Fig. 13A; *R*₃ of Comstock; cubital), between 2nd and 3rd longitudinals.

First posterior cell (*V* in Fig. 13A; *R*₅ of Comstock), between 3rd and 4th longitudinals. The anterior cross-vein (*r-m*) cuts off the basal portion as the *first basal cell* (*1B* in Fig. 13A; *R* of Comstock; upper or anterior basal cell; Speiser's "vordere Basalzelle").

Second posterior cell (*VI* in Fig. 13A; *M*₂ of Comstock), always combined with the discal cell in the Hippoboscidae. When present, the anterior basal cross-vein (*M*₃) cuts off the basal portion as the *second basal cell* (*2B* in Fig. 13A; middle or posterior basal cell; Speiser's "hintere Basalzelle").

AX, fourth axillary; *BA*, third axillary; *BAC*, basicosta; *CO*, costa; *DCL*, upper calypter; *EPL*, epipleurite; *h*, humeral cross-vein; *IA*, second axillary; *INC*, axillary incision; *NO*, first axillary; *PCL*, lower calypter; *PWP*, posterior wing process; *SC*, subcosta; *sv*, stem-vein; *TG*, tegula; *1, 2, 3* and *4*, first, second, third and fourth longitudinal veins. **E**, *Pseudolynchia canariensis* (Maequart); longitudinal section of salivary duct through valve, after Jobling (1926): *HYC*, hypodermic cells; *SD*, salivary duct; *SIV*, salivary valve; *SVM*, salivary valve muscles; *TA*, taenidia.

Third posterior cell (VII in Fig. 13A; *Cu* of Comstock). When present, the anal cross-vein (*ac*) cuts off the basal portion as the *anal cell* (AN in Fig. 13A; *1An* of Comstock; lower or third basal cell).

Axillary cell (VIII in Fig. 13A; *2An* of Comstock).

The chief venational differences between all Hippoboscidae and most higher Muscoidea are: (1) the lack of a discoidal cross-vein (*m* of Comstock; *se* or serial vein of Lower, 1951; medial cross-vein of Ferris, 1950; discal, posterior, medio-cubital, postical, or lower marginal cross-vein) between the 4th and 5th longitudinals apicad of the anterior basal cross-vein, so that no discal cell is closed off from the apical portion of the 2nd posterior cell; (2) the straight 4th longitudinal, which is never curved or bent forward at the tip into a subapical or hind marginal cross-vein setting off an "apical or subapical cell."

The axillary lobe or *alula* (*ALU*; alar lobe; Speiser's "Analappen"; proximal alar lobe of Snodgrass, 1935, p. 227) is usually well developed, more rarely reduced or lacking; when present, it is divided from the axillary cell by a deep *axillary incision* (*INC*) of the hind margin.

The membrane of the wing is either totally bare or partly or almost wholly covered, either on the upper or the under side or on both, with minute hairs or *microtrichia*. The extent of these hairy areas often provides useful specific characters, although it tends to vary somewhat within specific limits. Since microtrichia occur sporadically throughout the family, regardless of host associations, it is difficult to surmise what use, if any, they may have.

The major differences in the venation, such as the number of the longitudinal and cross-veins, are usually of generic value. Some of the main types are shown in Figs. 12A, 12G-I, 13A, and 14A-F. Minor differences, particularly in the position of the cross-veins and of the apices of the longitudinal veins, are often unreliable even as specific characters. The Melophaginae show the greatest reduction of the venation, although in the newly-emerged adults, or volants, wings are functional until the permanent host is reached. In *Hippobosca*, the wings are sturdier than usual; the veins are thick basally and anteriorly, and the membrane beyond them is closely wavy or corrugated, many delicate, more or less parallel or bifurcate wrinkles running toward the hind margin. Both features seem to be adaptations to life among the coarse hair of Ungulates and Carnivora, the chief hosts of *Hippobosca*, which has some of the most active fliers in the family.

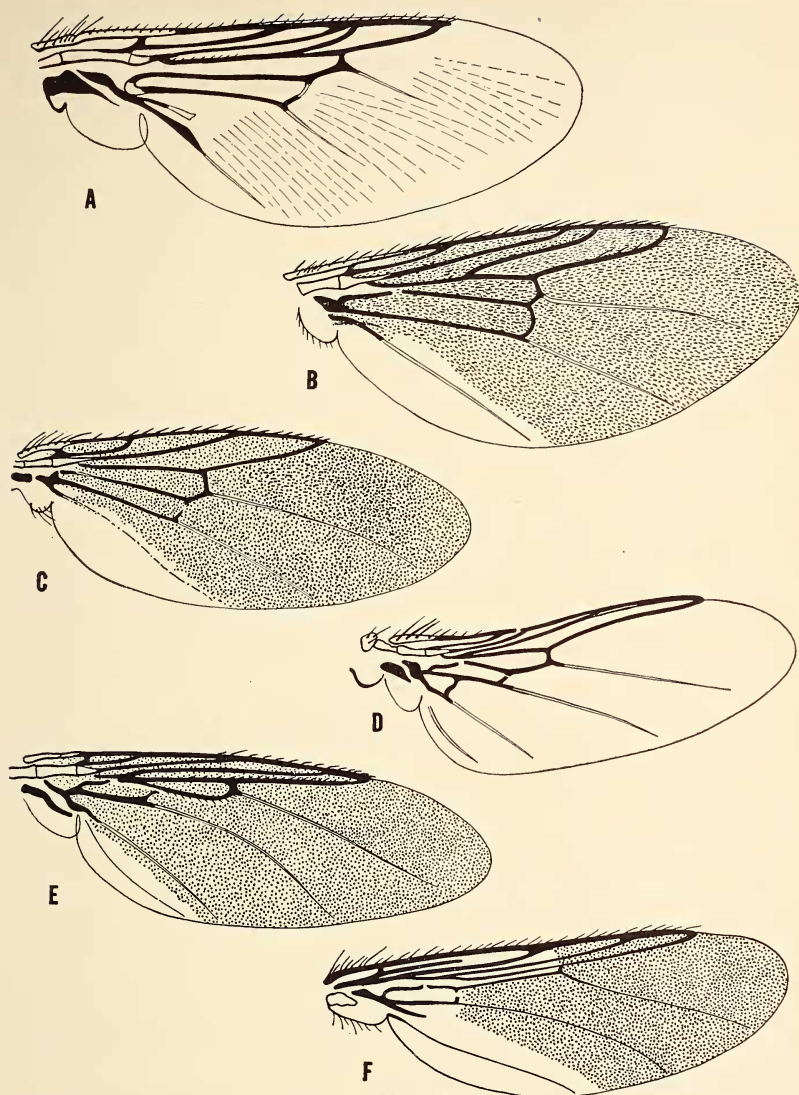


FIG. 14. Wings of Hippoboscidae: **A**, *Hippobosca rufipes* v. Olfers; **B**, *Ortholfersia phaneroneura* Speiser; **C**, *Austrolfersia ferrisi* J. Bequaert; **D**, *Ornitheza metallica* (Schiner); **E**, *Olfersia sordida* Bigot; **F**, *Lynchia americana* (Leach).

In many Diptera and particularly in the higher Muscoidea, the base of the wing membrane is connected with the posterior ridge of the parascutellum by means of two scale-like lobes, the *calypteres* (squamae or squamulae). (Snodgrass, 1935, p. 227, calls the combined upper and lower calypteres "alula"). The one nearest the alula, from which it is separated by a notch, is the *distal* or *upper calypter* (*DCL*; squamula alaris or superior); the other, inserted on the posterior side ridge of the parascutellum, is the *proximal* or *lower calypter* (*PCL*; squamula thoracalis or inferior). At rest, when the wings are directed backward or lie on top of each other over the abdomen, the distal calypter folds over the proximal one, so that the upper surface of the former comes to lie against the upper surface of the latter. Ad. Lutz, Neiva and da Costa Lima (1915, p. 174) first noted that calypteres are not completely lacking in all Hippoboscidae, as is sometimes claimed. In the majority of genera they are reduced in size and particularly very narrow. There is no trace of them in the winged Melophaginae, which also have no alula, as well as in the equally winged Ortholfersiinae; they are rudimentary in the winged Ornithoicinae. On the other hand, in certain fully-winged Ornithomyiinae, such as *Ornithoctona* (Fig. 13D), the lower calypter is fairly large, translucent but stiff, bordered by a thick *axillary cord* (*ACO*) bearing many long cilia; between it and the alula, separated at either end by distinct, broad notches, lies a very narrow membranous upper calypter, also briefly ciliated at the thin edge. In *Hippobosca*, the relative development of the two calypteres is reversed, the upper calypter being large and membranous (in fact more squamula-like than the lower calypter of *Ornithoctona*), while the lower calypter is very narrow. The difference between the two genera suggests that the reduction of the calypteres in the Hippoboscidae is not a primary condition, possibly retained from some common Muscoid ancestral stock, but rather a secondary feature, which recurred several times independently and not always in the same manner in the course of evolution. Most probably the ancestral stock of all louse-flies was a calypterate muscoid type, possibly one in which the calypteres were not as fully developed as in most Recent higher Muscoidea and particularly as in the Glossinidae.

Axillary sclerites (alar ossicles or pteralia) may also be traced in the winged Hippoboscidae (Figs. 12J and 13D). The *tegula* or epaulet (*TG*), at the extreme upper base of the wing, is scale-like and usually setulose. This is followed by the short and bare *basicosta* (*BAC*; subepaulet or parategula), on which the swollen basal

section of the costa is inserted. Immediately behind the tegula lies the *first axillary* (*NO*; notopterale), often partly divided by transverse sutures, and, between this and the stem vein of the first longitudinal, the *second axillary* (*IA*; intraalare). Behind these, two closely associated sclerites form the *fourth axillary* (*AX*; adanale), at the tip of the *posterior wing process* (*PWP*). The *third axillary* (*BA*; basanale) is a strong sclerite connecting the fourth axillary with the thickened base of the axillary vein.

Halteres (*HA*) are present in all winged Hippoboscidae, even those with reduced or functionless wings; they are absent in the two completely apterous species of *Melophagus*. They are relatively short for the fly's size and about the same size in both sexes. Contrary to published statements (Massonat, 1909, p. 79; Fraenkel, 1939, p. 75), they are not appreciably reduced in the subapterous species. Brauns (1939) gives the length (in mm.) of those he examined as follows: *Ornithomyia avicularia*, ♀ 0.479, ♂ 0.571; *O. fringilina*, ♀ 0.504, ♂ 0.445; *O. biloba*, ♀ 0.420, ♂ 0.437; *Lipoptena cervi*, ♀ 0.378 to 0.471, ♂ 0.377 to 0.462; *Stenopteryx hirundinis*, ♀ 0.420, ♂ 0.395; *Crataerina pallida*, ♀ 0.496, ♂ 0.487. They differ little in shape from those of other Diptera and occupy the same position as in the higher Muscoidea, but are never hidden from view by the calypteres. Each halter (Fig. 13C) consists of a moderately widened, conical base or *scabellum* (*sca*), followed by a short, slender *stalk* (*sta*) bearing a relatively broad and short, hammer-shaped *knob* (*kn*). According to Roberts (1927) and Brauns (1939), the basal portion of the stalk is provided with a pair of sclerotized integumental rods, one anterior, the other posterior, which are connected by a row of transverse braces, giving it a striated appearance (Fig. 13B). This structure is peculiar to the ectoparasitic Pupipara and Brauns believes that it prevents further injury to the base of the halter in case the knob breaks off while the fly moves in the plumage or pelt of the host.

For flight the fully developed wings spread horizontally; at rest they lie flat over each other on the back of the abdomen, like closed scissor-blades, a characteristic position they share with those of the tsetse-flies. In species where they are reduced and no longer used for flight, they are immovable and cover the halteres, which they may help protect.

The integument of the abdomen is mostly soft and extensible, the hardened sclerites being dorsally more or less reduced in size or number and ventrally small or almost lacking. Adult Hippoboscidae may be said to be physogastric from the time they emerge,

the soft areas of the integument merely stretching as feeding proceeds or as the larva grows in the uterus. The true *first tergite* (*TER1*), nearly always present, forms a pair of *laterotergites*, bearing the first pair of *abdominal spiracles* (*SP1*) near the base, the corresponding median area having seemingly disappeared. These laterotergites are either free or fused in part or wholly with a basal median tergal plate (true 2nd tergite; *TER2*) or with the second laterotergites, when either of these are present. The sclerotized portions of the succeeding tergites are generally reduced to the median plates, varying in number, relative size and shape and thus offering reliable specific and even generic characters. The maximum number of median tergal plates observed in the family is five (in *Ornithoica*), the basal one being the true second tergite as shown by its relation to the second pair of spiracles (*SP2*). At the apex a few small sclerites occur near or around the anal and genital openings, both dorsally and ventrally. A distinct ventral sclerite or *first sternite* (*STR*) is often present at the base of the abdomen. In some genera, such as *Hippobosca* and *Myiophthiria*, all sclerites, except the basal ones are greatly reduced or lacking, even dorsally, the original segmentation of the abdomen being then indicated only by the position of the spiracles. The spiracles being often difficult to trace, some authors, such as Dufour, were led to believe that the Hippoboscidae lacked all segmentation of the abdomen; in the more generalized *Ornithoica* the dorsal segmentation is as distinct as in many Muscoidea. It should be kept in mind that in a newly emerged hippoboscid the soft, membranous integument of the abdomen is greatly contracted or shrivelled, so that the sclerotized parts are crowded together or even overlap, and may appear to cover most of the surface. The soft areas expand, spreading out the several sclerites, after feeding in both sexes, and even more in the female as the larva grows in the genital tract. The appearance of the body is thus completely altered, sometimes deceiving the observer into thinking he has to do with a different species. Moreover, the hardness and color of the sclerotized areas may also change in the same individual during life.

The terminal abdominal segments, or *terminalia*, are poorly differentiated and relatively unimportant for taxonomic purposes in this family. In the unfed, non-pregnant female the *anal opening* (*ANO*), at the hind extremity of the body, occupies the center of the *anal tergite* (*ANT*), a broadly elliptical or subcircular sclerite at least partly surrounded by a raised rim. Immediately beyond lies the *vulvar opening* (*VUO*; female gonopore), usually a trans-

verse slit between two small, finely setulose, sclerotized *genital plates* (*GEP*), one anterior, the other posterior. Since, according to Crampton (1942), the female gonopore is located between the eighth and ninth segments, the anterior genital plate may be the modified eighth and the posterior genital plate the modified ninth abdominal sclerite. The *male* copulatory organs or *external genitalia* were first described and figured by Réaumur (1738, p. 159; Pl. 11, fig. 4) for *Stenopteryx*. They are usually placed ventrally and simpler than those of most higher Muscoidea, being reduced to five pieces, possibly representing the gonocoxites, penis valves and penis of other Diptera, although the homologies may be disputed. For my present purpose I adopt Michener's (1944) terminology, without expressing an opinion as to the validity of his homologies. The *gonocoxites* (*GCO*; basal segments of the outer claspers; Cole's genital styles; paralobes of Zumpt and Heinz) are a pair of sclerotized, bristly, lateral lobes or knobs, either sessile or stalked and sometimes very short, inserted on a small, median, horseshoe-shaped sclerite (ninth sternite), beyond the anal opening. They are periphallic (or pseudophallic) organs and merely cover or protect the aedeagus, which when not in use may be retracted almost completely within the notch of the horseshoe. They reach their greatest development in *Olfersia* and are atrophied in *Melophagus*. The *aedeagus* (*AED*) comprises the true phallic (or euphallic) organs, derived from appendages of the tenth segment. It consists of a basal ring or common stalk, the *caulis* (*CAU*) or theca (Hennig's "Gabelplatte"), supporting three elongate pieces of nearly equal length: a median, cone-shaped or rod-like *penis* proper (*PE*; intromittent organ or phallus; Cole's aedeagus; penis sheath of Roberts) and two hard, thickened and pointed *penis valves* (*PEV*; parameres or gonapophyses of authors; Cole's interior forcipes; claspers of Roberts), one to each side of the penis. The terminal portion of the penis is hinged to a broad *supporting piece* (*SUP*; Hennig's "Tragplatte"), itself connected basally with the caulis. While morphologically speaking the vulvar opening and the male terminalia are behind the anal opening, they are almost always in a ventral position in the Hippoboscidae, so that in a ventral view they appear to lie basad of the anal sclerite.

When the abdomen is not too distended by food or by a developing larva, the terminal median sclerites are often retracted in a deep apical notch, so that the body appears to end in two broad lobes. This is sometimes rather striking, though not truly charac-

teristic either of the family or of any of its constituents; nor can it be relied upon to distinguish the sexes.

The number and position of the *abdominal spiracles* (SP1 to SP7, Figs. 16A–B) often are given incorrectly for the Hippoboscidae, although Lyonet (1829; 1832) recognized 7 pairs in *Melophagus ovinus* more than a century ago. Massonat (1909, p. 174), for instance, credits the entire family with 5 pairs only, while other authors have given various numbers for the several genera. Roberts (1927, p. 17) gives 5 pairs for *Hippobosca*, but I was able to locate 7 pairs in this genus. F. R. Cole (1927, pp. 452–453) found 7 pairs in *Lynchia americana*, *Lipoptena mazamae*, *L. gracilis* (= *L. traguli*), and *Melophagus ovinus*. Schuurmans Stekhoven (*in litt.*, 1952) located 7 pairs in *Pseudolynchia canariensis*. In all the genera where I attempted to trace them, I have found 7 pairs, though sometimes with difficulty. Although I have not examined all the known genera, I feel certain that 7 pairs is the normal number throughout the family. The position of the spiracles and their connection with the tracheal system are shown for *Melophagus ovinus* by Webb (1945), two of whose excellent drawings I have copied with the author's permission (Figs. 16A–B). Possibly some of the abdominal spiracles may be functionless in certain genera, as they are often very small and seem to lie sometimes just beneath the integument, apparently without outside opening. In such cases particularly, they are apt to be removed with the tracheal system when the abdomen is cleared by maceration and washing, preparatory to mounting on a slide. The first two pairs lie sometimes free on each side in the ventral integument; more often one or both of them are included in the sclerotized first and second laterotergites, which makes them particularly difficult to find. The succeeding pairs are usually placed in the membranous sides of the dorsum; the last two pairs are often close to tergal sclerites or one of them may even be included in them (*f. i.*, in *Hippobosca*); but the 6th and 7th pairs never occur together in the 6th tergite, as is sometimes the case in the higher Muscoidea. Malloch (1929, p. 553) pointed out that, in the Glossinidae and Gasterophilidae, the abdominal spiracles 1 to 7 lie in the membrane between the tergites and the sternites; in other calyptrate Diptera at least spiracles 2 to 5 are located in the sclerotized laterotergites. In view of the close relationship of the Glossinidae and Hippoboscidae, it is interesting to note that, in *Ornithoctona*, spiracles 1 to 7 also lie in the membranous sides of the abdomen, although this is not true for all spiracles in other genera. Moreover, it is doubtful whether the

location of the spiracles either in the membrane or in the sclerites has much significance, since most of the original laterotergites have clearly been lost in the Hippoboscidae, thus placing the spiracles secondarily again in the membrane.

The hairiness or *pilosity* depends on the number of setae and hairs, as well as on their length and texture, three factors which do not necessarily work in the same direction to produce the final appearance. The most hirsute hippoboscid is the apterous *Melophagus*, which is fairly evenly setose all over; even here the body setae are not actually more numerous than in many higher Muscoidea (Glossinidae, *Calliphora*, *Musca*, etc.); they are merely longer and particularly stiffer. In other subapterous and flightless genera, large areas, particularly of the thorax, are completely bare and the hirsuteness results from the overdevelopment and stiffness of the remaining setae. The fully-winged genera differ from these mainly in that the setae are only moderately long. In most cases, however, the setae of the thorax and legs are stiff and bristle-like, while those of the abdomen are softer and shorter. The general stiffness of the setae often obscures the orderly arrangement, or *chaetotaxy*, of the longer bristles (so-called "fixed setae" or *macrochaetae*), which is such an important feature of the Myioidaria. Some of the customary bristles may nevertheless be recognized in most genera. On the head, the innermost area of the inner orbit bears one or more rows of *orbital bristles* (*orb*; frontal bristles of authors), while near each outer corner of the postvertex are placed at least one, rarely two or more *vertical bristles* (*vb*; post-vertical bristles of authors); a row of small bristles may be present ventrally also along the oral margin and there may be a short median row or group of setae on the gula close to the occipital foramen. On the dorsum of the thorax, a few *acrostichals* (*idb*) and *dorso-centrals* (*hdb*) are sometimes present, as a rule posteriorly; or there are instead transverse rows or groups of *latero-centrals* (*lcb*) or *prescutellars* (*psb*), as for instance in *Lipoptena* (Fig. 11A). *Notopleurals* (*nob*), *postalars* (*pab*) and *supraäalars* (*sab*) can often be traced; the *presuturals* (*pb*), when present, are usually placed far forward. The scutellum bears a preapical row of *scutellars* (*scb*). The *humeral bristles* (*hb*), on the humeral callosities, may be few (as in *Lipoptena*) or many, in the latter case showing no definite pattern. The *mesopleurals* (*mpb*) either are placed dorsally on the anepisternum in one or more irregular rows before the base of the wing, or there are one or two only at the outer hind edge. The sides of the thorax are usually almost bare, except sometimes for

a posterior downward row of *mesopleurals* (*mpb*) and a few setae seemingly corresponding to the posterior *sternopleurals* (*stb*), though not in any definite arrangement. There may be even a group of setae on the sclerite between the hind coxa and the metathoracic spiracle, where the *hypopleurals* (*hpb*) are located in many Muscoidea; these are never placed in rows and are possibly not homologous with true hypopleurals. The swollen pleurotergites often bear setae, sometimes in a conspicuous vertical row (as in *Hippobosca*). The sternum is either nearly bare or more or less setulose and there is often a tendency for the setae to form longitudinal or transverse patches or to be crowded toward the sides, particularly near the coxae. The legs are usually also very hirsute, but show only exceptionally outstanding characteristic bristles. In most Hippoboscidae the abdomen is fairly uniformly and densely covered with short or long setae; some species have characteristic bare areas, which in *Lynchia* are densely covered with a microscopic transverse striation. In addition some parts of the abdomen may bear more prominent bristles or there may be definite numbers of setae in rows or groups on the well-defined sclerites. In most genera only the costa of the wing is setulose. In a few (*Olfersia*, *Hippobosca*), some other longitudinal veins, either the third or the fourth, are partly setulose; but the stem vein, or common base of the 1st, 2nd and 3rd longitudinals, never bears setae. The body hairs are never erect, but either slant more or less backward or are closely appressed against the integument, an arrangement allowing the fly to glide swiftly within the plumage or pelt, while keeping it from dropping out when the host is in motion. The setae are always stiff and occasionally even spine-like; they are never flattened nor arranged in regular and dense comb-like rows (etenidia), such as are found in many Streblidae and Nycteribiidae. The nearest approach to such an arrangement is on the apical scutellar margin of *Stilbometopa*. All bristles or setae of the Hippoboscidae, whatever their size or stiffness, are set in sockets provided with a nerve ending, so that they function as tactile sensoria. True hairs, or purely cuticular productions of the outer body wall, are rare, sometimes at the outer margins of the wings or scattered as microtrichia over the wing membrane. Ferris (1930, p. 70) called attention to peculiar patches of dull pollinosity on the head and thorax of *Lynchia*, *Pseudolynchia*, and *Olfersia*, which appear as if dusted with gray powder. With the proper magnification the patches may be resolved into closely packed, minute hairs, which produce the pollinose appearance by dulling the reflected light.

In the Hippoboscidae the integument of head and thorax is unusually tough, strongly sclerotized, leathery and resilient, so that the body can withstand much pressure without harm. These features are particularly pronounced in *Hippobosca* and even more so in *Melophagus*, the latter being almost impossible to crush with the fingers.

Coloration. The body colors of most louse-flies are dull and form poorly defined markings. Their various shades and patterns are of less diagnostic value than in almost any other group of Diptera. Unfortunately, most of the older descriptions are based on color alone, often ignoring completely the true structural characters, so that many species cannot be recognized without a study of the types. Color varies not only individually within the same population; it may also change in the same specimen under the influence of extraneous factors. Usually the integument is fairly uniformly pale gray or testaceous in the newly emerged fly; soon afterward some areas of head and thorax, as well as the sclerotized plates of the abdomen, darken to various shades of brown, blackish or mahogany-red. Some species gradually turn darker all over, either through aging or on certain hosts, possibly due to damper or cooler local climatic conditions, or to differences either in the type of blood available as food or in the color and texture of the hosts' plumage or pelt. Thus *Ornithomyia fringillina* tends to be lighter on passerines and decidedly darker on certain other hosts, notably on gallinaceous birds. There is no evidence, however, that these individually acquired color differences are in any way inherited or of racial value. With the very low degree of host specificity of *O. fringillina*, some of the offspring of the darker flies of game birds may be expected to reach eventually some song bird, on which they will revert to the paler type. Much could be done in this particular field by controlled experiments on a sufficiently large scale. Cowan (1943, p. 182) noted the color changes of individual *Lipoptena depressa* in British Columbia: "In the spring and early summer it is possible to distinguish the survivors of last year's brood from the new brood, even pregnant females, by the more intense pigmentation of the older individuals,—they look brown and weather-beaten beside the new batch." It should be emphasized that Cowan found both light and dark keds living side by side on the same individual host.

In most species of certain genera, the integument is very dark, either reddish-brown (*Hippobosca*) or black (*Ornithesa*, *Olfersia*, and *Lynchia*), sometimes with a light metallic greenish or bluish

sheen. *Hippobosca* is, in addition, unusual in the family in being ornate with ivory-white or pale-yellowish spots on head and thorax, the resulting regular pattern being to some extent specific, though not always fully reliable. Roberts (1927, p. 12) remarked that in newly-emerged *H. equina* the whole color scheme is much lighter throughout, the markings being distinct, but that these become less so as the insect gradually assumes a darker hue.

A more unusual peculiarity of certain Hippoboscidae is the dull grass-green color they show over the paler areas of the integument during life and for some time after death. The green coloring matter resides not in the integument, but in the circulating haemolymph, so that it appears only where the cuticula is not too heavily pigmented. The physiological aspects of this feature will be discussed later in connection with the circulatory system. The green eventually fades away after death in dried flies and disappears even more rapidly from specimens kept in a fluid. It persists longer in the legs and is sometimes seen also in the lighter stretches of the wing veins. It has not been observed in any of the louse-flies of mammals and, among the bird-flies, is known thus far only from the following genera of Ornithomyiinae: *Ornithomyia*, *Ornithoetona*, *Crataerina*, *Myiophthiria*, and *Stenepteryx*.

The first mention of the dull green color in a hippoboscid was by Réaumur (1738, p. 158) for *Stenepteryx hirundinis* of European swallows. He states in the "Explanation" of the figures of his "spider-fly of swallow's nests," readily recognizable as *S. hirundinis*, that the abdomen and thorax are usually dark green.² The greenish tinge of this species was apparently not mentioned since in print. Mr. G. E. Woodroffe, in England, who observed both *S. hirundinis* and *Crataerina pallida* alive, informs me (*in litt.*, 1952) that unfed adults of these species bred in the laboratory never showed any green color upon emerging or afterward when kept unfed. On the other hand, adults collected from nests were often greenish, particularly on the femora; some specimens were more strongly colored than others and these may have been flies that had fed more recently.

Slabber (1768) seems to have been much impressed by the color differences of the three specimens of *Crataerina pallida* (his "ge-vleugelde zesendertig-tengelige vogel-luis," as is evident from the figures), which he kept alive for some time. One was pale-green ("licht-groen") over parts of the abdomen, thorax, head and legs;

² "Communément leur corps et leur coreelet sont d'un vert foncé."

another showed only a trace of greenish color; the third lacked it altogether. The green color of *C. pallida*, the common parasite of European chimney-swifts, was mentioned by several later authors: Massonat (1909, p. 322), Austen (1926, p. 353), Falcoz (1926, p. 36), Kemper (1951, pp. 232-234), and no doubt others. In describing another species of the genus, *C. obtusipennis*, Austen (1926, p. 356) mentioned that a greenish tinge was sometimes distinctly visible here and there in the legs. It may safely be assumed that the greenish color appears in all members of the genus *Crataerina*.

Myiophthiria, with which I unite *Brachypteromyia*, is a close relative of the two preceding genera and occurs on the same type of hosts. It may be expected to show greenish color also; owing to the difficulty of obtaining live specimens, the color has been observed in one species only. W. Beebe (1949, *Zoologica, New York*, **34**, pt. 2, 61) noted in Venezuela that the abdomen of *M. (Brachypteromyia) neotropica* was "bright sage green" in life.

Green has most often been reported for species of *Ornithomyia* and is probably universal in this genus. Degeer (1776, p. 285) first noted it in *O. avicularia*, stating that body and legs were green, except for the black and shiny thorax. The specific names of two of the synonyms of *avicularia* refer to the greenish color: *Ornithomyia viridis* Latreille (1805) and *Ornithomyia viridula* Meigen (1830). This feature is mentioned in both descriptions and the authors, unaware of its sporadic and transitory nature, seem to have been unduly influenced by it and by Linnaeus' failure to mention it when describing *avicularia*. Curtis (1836) described his *O. fringillina*, in England, as "ochreous, inclining to bright green"; Say (1823), in describing his *Ornithomyia pallida* from North American specimens of *fringillina*, noted that the tarsi were tinged with green. The specific name of Bergroth's *Ornithomyia chloropus* (1901), another synonym of *fringillina*, again refers to the verdigris legs; it is stated, in addition, that the head was mostly pale green beneath and the abdomen greenish-yellow. Dufour's (1827) original description of *O. biloba* likewise stated that the abdomen had a greenish tinge, which disappeared by drying, and that the legs were a livid greenish-gray. Schiner (1864) said of his *O. tenella*, which I regard as a synonym of *biloba*, that the thorax was greenish or yellowish and the legs horn-yellowish or pale green. The green color has been so often noted in the foregoing three Old World species that it seems superfluous to cite more references. The South American *O. remota* Walker (1849) may also be partly greenish. E. C. Reed (1904) emphasized that in his *Ornithomyia chilensis*, a synonym of

remota, "green prevails in life and black after death, because the green occurs in the soft integument between the coriaceous plates and is more apparent before the insect shrivels and dries. Green is more extensive on the under side, as well as on the legs. The extent of this tinge varies greatly among the specimens." Bigot (1885) mentions the greenish color in the description of his *O. fuscipennis*, a species supposedly of Colombia, but as yet unrecognized.

In *Ornithoctona*, the greenish color is a well-known feature of the common American *O. erythrocephala*, mentioned by Leach (1817) in his original description for the under side of the head, the sternum and the legs beneath ("sordide viridescence testacei"). However, in his type, at the British Museum, the greenish areas have now turned to a dirty pale-yellow. Newstead (1909, p. 467) noted the vivid green tinge of this fly in life. The descriptions of the following synonyms of *erythrocephala* mention greenish areas: *Ornithomyia laticornis* Macquart (1835) and *Ornithomyia costaricensis* Swenk (1916). The second common American species of the genus, *O. fusciventris*, shows the same color feature, the legs being originally described by Wiedemann (1830) as mostly green. It was also mentioned in the descriptions of the following synonyms of *fusciventris*: *Ornithomyia parva* Macquart (1843), *Ornithomyia varipes* Walker (1849), *Ornithomyia synallaxidis* Lynch-Arribálzaga (1881), and *Ornithomyia pirangae* Swenk (1916). The Indo-Malayan *O. plicata* also is often blotched with green, although this was not mentioned by v. Olfers (1816) in the original description. It was noted, however, by later authors who redescribed the same species under new names: Leach (1817) for his *Ornithomyia nigricans*; Wiedemann (1824) for his *Ornithomyia columbae*; Guérin-Méneville (1831) for his *Ornithomyia australis*; Boisduval (1835) for his *Hippobosca sitiens*; Macquart (1851) for his *Ornithomyia asiatica*; Walker (1858) for his *Hippobosca viridipes*; Walker (1861) for his *Ornithomyia doreica* and *Ornithomyia batchianica*. The African *O. platycera* also may be partly greenish, as Macquart (1843) mentioned in the original description. One of the specimens of *Ornithoctona* (*Ornithopertha*) *nitens* I have seen from Costa Rica had the femora distinctly greenish several years after it was collected and had been kept dry.

INTERNAL ANATOMY AND PHYSIOLOGY

I. **Internal Appendages of the Integument.** Various folds or ingrowths of the body-wall form the rods, ridges and knobs of the endoskeleton, which either strengthen the exoskeleton or act as levers

or apodemes for the muscles. In the Hippoboscidae such ingrowths are unusually developed in the thorax, because its dorso-ventral flattening has resulted in a great extension of the exoskeleton. They should not be mistaken for external features when macerated and cleared specimens are examined in slide mounts. The internal appendages of the head are particularly important, as they constitute the hyoid and tentorium, which act as levers for the projector and retractor muscles of the proboscis.

II. Muscular System. The head contains ptilinal muscles, which retract the ptilinal sac within the head after the fly emerges; as well as antennal, proboscidal, suction (or cibarial), and salivary valve muscles. In the winged Hippoboscidae the thoracic muscles are all mesothoracic: six pairs of longitudinal dorsal muscles over the whole length of the dorso-central area (dorsad of the proventriculus) and three pairs of vertical or slightly oblique sterno-dorsal muscles along the sides of the dorsals. Both sets act indirectly upon wing motion by changing the size and shape of the thorax. There are also many smaller muscles moving the neck (cervicals) and the abdomen (thoraco-abdominals), as well as powerful coxal muscles moving the legs as a whole. In the wingless *Melophagus* sterno-dorsals are wanting, while dorsals are either wanting (according to Cuénot and Mercier) or much reduced and functionless (according to Massonat). Inside the leg segments, sets of muscles move the several pieces, either flexing or extending them, or drawing them forward or backward. Most Hippoboscidae are powerful and rapid runners, but rather slow fliers, even when the wings are fully developed. The abdominal muscles are relatively unimportant in these flies and mostly associated with the respiratory movements, the digestive tract and the reproductive system, particularly the terminalia. Webb (1945a) describes them in detail for *Melophagus ovinus* in connection with the respiratory mechanism.

The muscular system was studied in *Melophagus* by Dufour (1845), Massonat (1909), Cuénot and Mercier (1922), Jobling (1926), and Webb (1945); in *Lipoptena* by Massonat (1909) and Mercier (1924); in *Pseudolynchia* by Massonat (1909) and Jobling (1926); in *Ornithomyia*, *Crataerina*, and *Hippobosca* by Massonat (1909).

III. Nervous System. The nervous system of adult Hippoboscidae agrees in general with that of the Myiophoridae. The central nervous system comprises: (1) a large *cephalic ganglion*, or brain, perforated by the oesophagus and innervating the structures and sense organs of the head; (2) a voluminous *thoraco-abdominal*

ganglion, in the anterior region of the thorax close to the mesosternum, connected anteriorly with the cephalic ganglion by the *cephalo-thoracic cord*; it sends nerves to the inner and outer parts of thorax and abdomen. In addition, a *splanchnic system*, consisting of a proventricular ganglion and connected with the cephalic ganglion, innervates the viscera.

The *sense organs* comprise: (1) organs of *sight*, the compound eyes and ocelli, described before. Little is known of visual perception in the Hippoboscidae. In the normal life of the fly it seems to play a minor rôle, perhaps discriminating only degrees of luminosity. Negative phototropism may to some extent induce the flies to hide in the feathers or hairs, although this behavior is chiefly conditioned, it would seem, by tactile stimuli. Gravid females definitely search for dark places in species leaving the host for larviposition. On the other hand, when alarmed or forced to leave a dead host, the flies are positively phototropic, tending indoors to fly toward window panes. Perception of moving objects, only a response to differences in light intensity and a rather crude method of orientation, may sometimes guide the flies toward a potential host, for instance after they emerge from puparia dropped at random. There is no evidence that louse-flies distinguish definite objects, either by shape or by color.

(2) The organs of *smell* or *olfactory pores* are in most insects located mainly on the third antennal segment and palpi. As I have pointed out, the greatly reduced and concealed third antennal segment suggests that the sense of smell is of relatively little importance in the life of the Hippoboscidae. K. M. Smith (1919, p. 64, fig. 43) found that the third antennal segment of *Ornithomyia avicularia* has no true sense-pits, such as are found in the Muscoidea, but only slight depressions in the surface with a few thin sensory processes. These insects also have no known scent glands and give off no odor detectable by man.

(3) In the Muscoidea, the organs of *taste* are usually located on the labella of the mouth-parts and on the tarsi. It is doubtful that they are much used by louse-flies, which live under conditions where only one type of food, namely blood, can be reached by the mouth-parts. Any preliminary probing of the skin, before actual feeding, is probably regulated mainly by touch and perhaps partly by smell.

(4) The organs of *touch* consist of many tactile setae on the palpi, the second antennal segment, the dorsum of the thorax, the legs, the costa and various other parts of the body. To judge by the

abundance and size of such receptors, it would seem that touch outweighs all other senses in normal hippoboscid life.

According to Schellhase (1921) and Hase (1927b, pp. 199-205), when *Hippobosca equina* is deprived of sight and smell by decapitation, it survives for some time, as long as circulation and digestion function. In Hase's experiments such a fly remained alive away from a host at 22° to 25° C., for 3 days in a dry atmosphere and up to 9 days in a moist chamber, survival comparing favorably with that of a normal insect. It did not attempt to fly and remained practically motionless, being deprived of means of orientation, but held on firmly to the support by the claws. When turned over, it resumed the normal position by throwing the body forward over the anterior margin of the thorax, showing that the ventral surface is positively thigmotropic. It is most interesting that it reacted to a heated glass rod, moved near the wings or hind legs, by lively cleaning motions applied to these parts.

The Hippoboscidae have a keen temperature sense, evidenced by their quickly leaving the cooling body of a dead host. Martini (1916, *Lehrbuch Medizinischen Entomologie*, 3rd Edition, p. 268) and Hoffman, Roth and Lindquist (1950) noted that at a higher ambient temperature *Melophagus ovinus* migrates away from the skin of sheep to the outer wool. Herter (1952, p. 144-145 and 151-152) determined experimentally what he calls the preferred temperatures of *Melophagus ovinus*, *Hippobosca equina*, *Lipoptena cervi*, *Ornithomyia avicularia*, *O. biloba*, and *Crataerina pallida*, using unfed flies away from the host. They were on the whole close to the normal skin temperatures of the normal hosts, the slight differences observed having scarcely the ecological importance which the author seems to claim for them. Thus the preferred temperature of *M. ovinus* was 37.89° C., while the surface skin temperature of sheep is 36.5° to 38.5° C. His experiments show that a temperature sense is highly developed in these flies. Prouty and Coatney (1934) found that *Pseudolynchia canariensis* (= *P. maura*) has a decided humidity sense, the presence of moisture being very repellent. That the flies, if kept away from a suitable host, survive longer in a moist than in a dry atmosphere, was observed for *Hippobosca equina* by Hase (1927b) and for *Melophagus ovinus* by Sweet and Seddon (1917). The sensory mechanism of heat and moisture stimulation is as yet little known in insects. A few species seem to have special thermoreceptors and hygromoreceptors; but no such sensoria have been located in any of the louse-flies.

Prouty and Coatney (1934) studied various other tropisms of

Pseudolynchia canariensis. They found that this fly is positively thermotropic and thigmotropic, and negatively phototropic and hydrotropic. According to Cowan (1943), newly-emerged, winged *Lipoptena depressa* display a strong negative geotropism, always moving upward; also a pronounced positive phototropism, secondary however to the negative geotropism, but no positive thigmotropism. On the other hand, deälated keds, which have fed for some time on a deer, show a strong positive thigmotropism, that causes them to cling to any small object and to each other.

(5) *Chordotonal* and *campaniform* (or dome-shaped) sense organs are present on some of the wing veins, both on the upper and under side, as well as on the halteres, of all Diptera, even of those that have lost the power of flight. The sensoria on the basal portion of the costa and on the halteres of *Lipoptena depressa*, which McIndoo (1918) interpreted as "olfactory pores," certainly belong in the present group. The innervation of the tactile hairs and chordotonal organs of the wing of *Crataerina pallida* was carefully studied by Zaćwilichowski (1934). He showed that, even in the atrophied and functionless wing of this fly, sensoria are as fully developed and as completely innervated as in some other Diptera with functional wings. Brauns (1939) found in *Ornithomyia*, *Stenepteryx*, *Crataerina*, and *Lipoptena* numerous dome-shaped sensoria on the base of the halteres, as well as on the swollen and slender portions of the stalk, the latter also bearing so-called Hicks' papillae; the knob itself usually lacks dome-shaped receptors, but bears instead a few short sensorial setae (Fig. 13C). According to Roberts (1927), the knob of the halteres of *Hippobosca equina* bears two tufts of sensorial setae.

The tactile setae and other sensoria of the wings and halteres of the Diptera appear to be proprioceptive organs, stimulated by the movements and internal strains of the body, and to influence also equilibrium during flight. This can hardly be disputed in the case of Diptera with fully-developed and functional wings. As I have pointed out, in 85 per cent of the species of Hippoboscidae the wings are fully developed and used for flight. In these the halteres have no doubt the same function as in other winged Diptera. There is, however, much difference of opinion as to the sensorial mechanism involved. It is particularly difficult to explain why the removal of the halteres impairs the faculty of flight in some Diptera, but not in others. Moreover, total amputation of one or of both halteres sometimes affects the ability to use the legs for walking or for resting in a normal position. The several theories offered in this con-

nection and the experiments carried out to prove or disprove them, have been ably reviewed by Brauns (1939; 1951), Melin (1941), Pringle (1948), and Eggers (1950). Pringle gives preference to the older view and regards the halteres as primarily organs of special sense, which by their vibrations act as alternating gyroscopes, thus helping maintain equilibrium in flight; they warn the fly specifically of unsteadiness and deviations from the right course. Evidently this explanation is hardly satisfactory for the subapterous, flightless Hippoboscidae (*Crataerina*, *Stenopteryx*, *Myiophthiria*, and *Allobosca*), in which the halteres not only show no great reduction, but are well provided with the usual types of sensoria.³ The theory which regards the halteres chiefly as stimulatory organs, contributing to the energy or tonus of muscular movements, might perhaps better fit their case. Melin generalized much the same concept by attributing to the halteres a general controlling nervous function in the physiology of flight, releasing what he calls "myodynamic reflexes." Eggers supposes a nervous coördination between the motions of the wings and of the halteres, which seems hardly more than a variant of the "stimulatory" theory.

It might perhaps be suggested that in the subapterous hippoboscids of birds, which are long-legged, unusually speedy runners, capable of swift changes of direction, forward, backward and sideways, the halteres regulate and coördinate the movements of the legs. It is remarkable that, in these flies, enough of the wing is preserved to form a protective covering for the halteres, so that these organs would seem to be essential for the normal life of the insect. On the other hand, the short-legged and completely wingless *Melophagus*, which also lacks halteres, is sluggish and merely crawls in the fur of the host. The "subapterous" *Allobosca* has short, swollen legs and well-developed halteres, and is a slow crawler; as all known specimens have been taken on the host, I suspect that its wing pads may be basal remnants of fully-developed, functional wings present in the newly-emerged fly.

The Hippoboscidae appear to have no functional organs of hearing, nor any devices or organs producing sound either in flight

³ Only the two completely wingless species of *Melophagus* lack halteres. It should be noted that the species of *Lipoptena*, *Neolipoptena*, and *Echestypus* are fully-winged and active fliers upon emerging from the puparia, and cannot be regarded as having reduced wings. I do not, therefore, include them among the subapterous hippoboscids. *Allobosca* is provisionally regarded as subapterous.

or at rest. At any rate, the normal flight of the winged forms is noiseless to the human ear. Hase (1927b, p. 193), however, noticed that *Hippobosca equina* buzzes when held by the legs in such a manner that the wings can move freely.

As in other insects, much of the so-called instinctive behavior consists of reflexes, tropisms and more purposeful activities in response to various external stimuli. For normal efficient life it is important that the sensorial receptors, through which the stimuli reach the central nervous system, be kept perfectly clean. Foreign matter should also be removed from legs and wings, if these organs are to function properly. The cleaning motions of the winged Hippoboscidae are similar to those of most other Diptera. Hase studied them in *Hippobosca equina* (1927b, pp. 196-198), which is very active in this respect, no doubt because life in a mammalian pelt exposes it continually to dirt. All the legs, in various combinations, are used to clean the legs themselves, the wings and every part of the body within reach. Particular attention is paid to the head, especially the eyes, and the wings. Shortly before feeding ends, the fly always makes some cleaning motions over the eyes and wings, indicating that it is about to leave the site of the bite. Otherwise cleaning is mostly in response to the presence of foreign matter on a given area. Heinz (1949, p. 359) found that the spontaneous cleaning motions of *Stenepteryx hirundinis* are of the same type, but very swift and skilful. This fly cleans itself as a rule immediately after being removed from the bird's plumage; the process is not repeated spontaneously later, but may be induced by powdering the body. Kemper (1951, pp. 253-255) described the cleaning process of *Crataerina pallida*. Observations by Freund and Stolz (1928), Heinz (1949, p. 358), and Kemper (1951, pp. 255-256) show that *Melophagus ovinus* is very indifferent to dirt: it does not clean itself spontaneously, except on the mouth-parts; even stimulation by heat or concentrated acetic acid only induces cleaning of the proboscis, exceptionally also of the eyes, with one or both fore legs, the proboscis or head usually bending then toward the moving leg.

The nervous system and sense organs were studied by Dufour (1844), Massonat (1909), and McIndoo (1918) in *Melophagus*; by Massonat (1909) in *Crataerina*, *Pseudolynchia*, and *Lipoptena*; by Dufour (1844), Massonat (1909), and K. M. Smith (1919) in *Ornithomyia*; by Dufour (1844; 1845; 1851), Ciaccio (1884), Massonat (1909), and Hase (1927) in *Hippobosca*. The sensoria of the wings and halteres were described by Hicks (1857; 1860),

Weinland (1890), and McIndoo (1918) for *Hippobosca*; by McIndoo (1918) and Brauns (1939) for *Lipoptena*; by Baus (1936; his "*Melophagus cervi*" was *Melophagus ovinus*, according to Brauns) for *Melophagus*; by McIndoo (1918) for *Lynchia americana* (as *Olfersia americana*); by Baus (1936) and Brauns (1939) for *Ornithomyia* and *Stenopteryx*; by Weinland (1890), Zaćwilichowski (1934), Baus (1936), and Brauns (1939) for *Crataerina*.

IV. Digestive and Excretory Systems. The digestive tract, very similar in all Hippoboscidae, consists of the usual main three regions (Fig. 15).

1. The *fore-gut* (stomodeum) comprises the mouth, the hyoid, the cibarial pump, the pharynx and the oesophagus. In the mouth-parts, the mouth proper, or buccal cavity, is the hollow tube of the haustellum.

The *pharynx* (*P*; Fig. 7A-D), or anterior, tubular portion of the oesophagus, runs through the cephalic ganglion in the head; an angular bend, with the apex directed forward, separates it from the *cibarial pump* (*CIP*), which is worked by special dilator muscles, drawing up the blood through the haustellum and pushing it back into the oesophagus. The cibarial pump connects with the hollow tube of the haustellum by means of an intervening tubular part of the buccal cavity, with sclerotized walls, comprising the *hyoid* (*H*). The *oesophagus* (*OE*) continues the pharynx as a slender tube, through the neck to about mid-length of the thorax. Here it opens in the mid-gut through a dilatation containing the cardiac valve (*CV*). Just before the valve, a tube opens on the ventral side of the oesophagus and extends backward into the basal portion of the abdomen, where it widens in a bilobed *diverticulum* (*D*), corresponding to the reservoir stomach or crop of other Diptera.

The diverticulum should be considered somewhat in detail, because of its possible rôle in feeding. It is greatly developed in the free-living hematophagous Diptera, such as the stable-flies and tsetse-flies, which use it to store large quantities of blood at one meal. It was overlooked by Dufour (1845) in *Melophagus*, *Hippobosca*, and *Ornithomyia*, and also by Roubaud (1909, p. 408, fig. 86) in *Melophagus*. Its existence in the Hippoboscidae was first recognized by Massonat (1909, pp. 159-164), who noted that it was more developed in the flies of birds than in those of mammals. In *Hippobosca camelina* and *Lipoptena cervi*, the canal is very narrow and the crop small (0.2 mm. long, 0.1 mm. high and 0.17 mm. wide in *L. cervi*); the canal is much wider in *Melophagus ovinus* and the crop is 0.25 mm. long; blood was never seen in the crop in these

genera. On the other hand, in the bird-flies *Pseudolynchia canariensis* (= *Lynchia maura*), *Ornithomyia avicularia*, and *Crataerina pallida*, the canal and bilobed pouch are much better developed (particularly in *Crataerina*) and blood is actually stored in the diverticulum. Massonat states that he saw frequently blood corpuscles in the crop of *Pseudolynchia*. Hoare (1923) confirmed these findings for *M. ovinus*; Theodor (1928, p. 289, fig. 6) for *Lipoptena capreoli* (= *L. caprina*), *H. camelina*, and *Hippobosca equina*; Adie (1915) for *P. canariensis*. These authors did not see blood in the diverticulum; Theodor noted that in *L. capreoli* it is sometimes filled with a yellowish liquid. According to unpublished observations by Mr. I. B. Tarshis (*in litt.*, 1951), in living *Stilbometopa impressa* the bilobed diverticulum is rather large, extremely dilated, with smooth, elastic, not plicated outer walls, and is at least partly filled with blood after each meal. Evidently it serves as an additional food reservoir in this species, which, nevertheless, uses also the expansible duodenum for the same purpose.

2. The *mid-gut* (mesenteron) consists of the proventriculus, ventriculus and duodenum. The *proventriculus* (PV), abruptly wider than the oesophagus, lies in the posterior portion of the thorax. It is essentially a *cardiac valve* (CV), being nearly filled with the thickened folds of the wall. Its structure is more complex in some genera than in others and its functions are not completely understood. The *ventriculus* (VE) extends over the hind half of the thorax into the base of the abdomen. The abdominal portion of the mid-gut is the *duodenum* (DU) and starts at the base of the abdomen as an abruptly widened, sausage-shaped, expansible portion, where blood is stored while feeding. This is followed by an unusually long tubular portion (6 to 7 times the length of the body), with post-imaginal growth in the Hippoboscidae; it describes several loops and opens in the hind-gut, in the distal region of the abdomen, just before the insertion of the Malpighian tubules. At the bend of the right-side loop, *Melophagus* shows a widened section with an area where the wall is thickened and contains a *mycetome* (*my*) of enlarged cells filled with symbiotic micro-organisms. Similar mycetomes have been found in all Hippoboscidae examined for the purpose. Their possible significance will be discussed later in connection with the feeding behavior. Aschner (1931, p. 394) mentions incidentally that the mid-gut contents of *Pseudolynchia canariensis* (= *Lynchia maura*) are enclosed in a peritrophic membrane. The presence of such a membrane in the Hippoboscidae was to be expected in view of its common occurrence in the Muscoidea

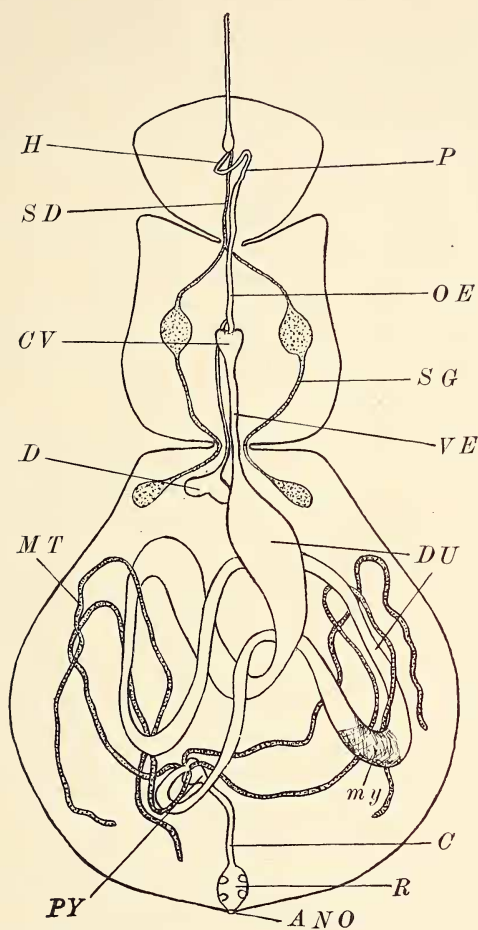


FIG. 15. *Melophagus ovinus* (Linnaeus), female; digestive tract and excretory system, modified after Hoare (1923b) and Anigstein (1927): ANO, anus; C, colon; CV, cardiac valve; D, diverticulum; DU, duodenum; H, hyoid; MT, Malpighian tubules; my, mycetome of mid-gut; OE, oesophagus; P, pharynx; PY, pyloric valve; R, rectum; SD, salivary duct; SG, salivary gland; VE, ventriculus.

(including *Glossina*), although it has been generally overlooked. The functions of the mid-gut are simultaneously those of digestion and absorption, the digested food products passing by dialysis through the walls of the gut into the body cavity. The process has not been studied in the Hippoboscidae. In *Glossina*, Lester and Lloyd (1928) and Wigglesworth (1929) describe a division of labor among the several sections of the mid-gut, the apical two-thirds only containing a powerful coagulin. One of the initial changes of digestion seems to be the rapid draining of water from the ingested blood, apparently by the Malpighian tubules. However, conditions observed in the tsetse-flies may not be strictly comparable to those of the louse-flies, at least in the species that do not use the diverticulum of the fore-gut as a true food reservoir, but store blood instead in the expansible basal portion of the mid-gut. Zacharias (1928, pp. 687-688) observed that, in engorged *Melophagus ovinus*, blood stored in the basal (or anterior) portion of the mid-gut retains its original color and fluidity. In the next two coils the blood is scarcely modified, only acquiring a more brownish-red tinge. Beginning with the right-side coil, where the mycetome is located, the blood is strongly altered, very dark brown to blackish, and clearly in the process of being digested.

3. The *hind-gut* (proctodeum) is relatively short. It starts with a funnel-shaped *pyloric valve* (*PY*), or ileum, where the Malpighian tubules open, followed by a tubular straight *colon* (*C*) widened posteriorly into a *rectum* (*R*), the inner wall of which bears four *rectal papillae*, or pulsating glands, jutting into the cavity. The rectum ends in the anal opening or *anus* (*ANO*). The function of the hind-gut is excretory, its wall extracting waste products from the blood of the fly's body cavity and diffusing them into the proctodeum. Very little material seems to reach it from the mid-gut after digestion. The rectal papillae have also a cardiac or circulatory function. Four main excretory organs, the *Malpighian tubules* (*MT*), are arranged in two pairs, one on each side, but without true common duct; each tubule is very long and thin, closed at the free end, and twisted throughout the adipose tissue of the body cavity. The contents of the hind-gut are always fluid.

The digestive and excretory systems were investigated in *Melophagus* by Ramdohr (1809; 1810; 1811), Lyonet (1829; 1832), Dufour (1844; 1845; 1851), Massonat (1909), Hoare (1923), Engel (1924), Anigstein (1927), and Zacharias (1928); in *Lipoptena* by Massonat (1909), Engel (1924), and Theodor (1928); in *Hippobosca* by Dufour (1825; 1844; 1845; 1851), Massonat (1909), Pat-

ton and Cragg (1913), and Roberts (1927); in *Ornithomyia* by Dufour (1844; 1845; 1851), Massonat (1909), and Zacharias (1928); in *Crataerina* by Massonat (1909); in *Pseudolynchia* by Massonat (1909) and Adie (1915). At present they are being studied most carefully in *Stilbometopa impressa* by Mr. I. Barry Tarsis, whose results will be published in the near future.

V. Adipose System. Dufour (1825, p. 320) first noted that the fat body of *Hippobosca equina* differs markedly in appearance from that of most other insects. His observation was confirmed and extended to other hippoboscids by v. Wielowiejski (1886, p. 522, for *Melophagus*) and others. According to Oektay's (1951) recent work, in the adult female of *Melophagus ovinus*, multinucleate cellular elements, arranged in loose moniliform or beaded strands, form a mesh throughout the body cavity of the head, thorax and abdomen. The cellular elements, each usually with an even number of nuclei, are of two kinds in the strands, most of them being filled with stored fat particles, but a few being without them. The adipose tissue of the male is mostly similar; the sexual organs are surrounded by a thin, continuous, one-layered sheath of cellular fat-containing elements of the more usual type. Oektay found much the same structures in *Melophagus rupicaprinus*, *Lipoptena cervi*, and *Hippobosca equina*, the differences being mainly in the number of nuclei in each fat-bearing cellular element. Massonat (1909) states that, in *Melophagus ovinus* and in deälated specimens of *Lipoptena cervi*, most of the longitudinal dorsal muscles of the thorax are replaced by adipose tissue. In addition to being used for storing superfluous fat, the adipose cellular elements may also have an excretory function and possibly other functions as yet unrecognized.

The adipose system was investigated in *Hippobosca* by Dufour (1825), Massonat (1909), and Oektay (1951); in *Melophagus* by v. Wielowiejski (1886), Berlese (1899), Massonat (1909), and Oektay (1951); in *Lipoptena* by Massonat (1909) and Oektay (1951); in *Ornithomyia* and *Crataerina* by Massonat (1909).

VI. Glandular System. Besides the excretory organs mentioned in connection with the digestive system (Malpighian tubules) and the circulatory system (pericardial cells), various organs secreting substances useful to the metabolism or the life of the insect occur throughout the body. They are connected either with the integument or with internal organs.

The most important of these are the *salivary glands* (SG; Fig. 15), built on the same general plan throughout the family. A pair

of blind, variously shaped expansions in the basal portions of the abdomen, just beneath the diverticulum, one on each side of the ventriculus, are the *excretory glands* (*EG*). Each sends off anteriorly a slender *salivary tubule* (*STU*), which, after entering the thorax, widens into an elliptical *salivary reservoir* (*SR*; Adie's goblet organ), after which it becomes tubular again. The two salivary reservoirs lie directly above the thoraco-abdominal ganglion, shortly behind and ventral to the cardiac valve. The distal portions of the salivary tubules next unite beneath the oesophagus into a common, usually coiled *salivary duct* (*SD*), which enters the neck. This finally connects at the bulbous base of the haustellum with the very fine tubular channel that runs the whole length of the stylet-like hypopharynx, opening close to its tip in the lumen of the haustellum. The general plan is the same as that of the salivary system of *Glossina* (Jobling, 1933, pp. 483-487, fig. XI, for *G. palpalis*), except that the tsetse-fly lacks the salivary reservoirs in the thorax. As in the case of the tsetse-fly, there is no true salivary pump in the Hippoboscidae, where the muscles of the walls of either the salivary reservoirs or the excretory glands, or of both, compensate for its absence; the contraction of these muscles squeezes the saliva through the ducts.

The structure of the salivary glands was studied most completely in *Stilbometopa impressa* by Mr. I. B. Tarshis, who has allowed me to quote the following details from his unpublished account. The excretory glands are definitely sausage-shaped, about $650\ \mu$ long and $80\ \mu$ wide. They seem to be attached to the wall of the under side of the diverticulum and are difficult to dissect out without severing their connection with the tubules, which are very narrow, about $8.23\ \mu$ in diameter. The thoracic salivary reservoirs are elliptical, with an average length of $453\ \mu$ and a greatest diameter of $190\ \mu$. The distal portion of the tubules is convoluted and the common duct also pursues a rather winding path. The diameter of the common terminal duct is approximately $4\ \mu$.

The details of the several parts vary somewhat in the other Hippoboscidae examined so far. The excretory glands of *Melophagus ovinus* are spherical expansions, according to Dufour (1845) and Massonat (1909, p. 149). Theodor (1928, p. 291, fig. 7) found them also spherical, about 0.25 mm. in diameter, in *Lipoptena capreoli* (= *L. caprina*). In the other genera, they appear to be sausage-shaped, as Massonat (1909) and Theodor (1928, p. 292, figs. 9-10) describe them for *Hippobosca equina* and *H. camelina*, Theodor adding that they are coiled around the mid-gut. Both

Massonat (1909) and Adie (1915, p. 674) found them sausage-shaped in *Pseudolynchia canariensis* (= *L. maura*). Massonat also examined them in *Ornithomyia* and *Crataerina*. Of *Crataerina pallida* (1909, p. 149) he states that the excretory gland ("tube excréteur") is in the thoracic region, strongly convoluted instead of straight; most probably he saw only the basal portions of the salivary tubules, the true excretory glands in the base of the abdomen being overlooked because they were severed in dissection.

Massonat (1909, p. 148, figs. 35 and 48) first noted that, in *Hippobosca camelina*, the common salivary duct bends shortly after entering the head, after which it suddenly widens and its wall now acquires inner spiral taenidia. The constriction at the bend has several muscles attached and functions as a *salivary valve* (SIV; Fig. 13E), regulating the outflow of the saliva from the duct into the hypopharynx: upon contracting, when the haustellum is protruded for feeding, they stretch the wall of the valve and open the lumen; upon relaxing, when the haustellum is retracted, the wall of the valve folds inward and closes the lumen. Cornwall (1923, pp. 1005-1007, figs. 14-15) describes this valve also for *Hippobosca*. According to Jobling (1926, p. 336, fig. III), the salivary valve of *Melophagus ovinus* is like that of *Hippobosca*; in *Pseudolynchia canariensis* (= *L. maura*) the basal portion of the duct, behind the valve, is also provided with spiral taenidia. Theodor (1928, p. 291, fig. 8) describes the salivary valve of *Lipoptena capreoli* (= *L. caprina*) as similar to that of *Pseudolynchia*.

The glands of internal secretion, *corpora allata* and *corpora cardiaca*, small cellular bodies in the head, generally at the sides of the fore-gut behind the brain and closely associated with the nervous system, are of special interest. M. F. Day (1943) found that *Melophagus ovinus* has two corpora allata in both adult and larva, lying one on each side of the dorsal aorta near the anterior part of the thoraco-abdominal ganglion in the adult and near the cerebral ganglia in the larva; they reach their maximum size during late larval development (third instar) and are considerably reduced in both pupa and adult. The corpus cardiacum is a single median organ not well developed in the larva, decreasing in the pupa and practically absent in the adult. No differences were found in the corpora allata of male and female, nor in females with and without developing larva. I have described these glands somewhat in detail because Day points out that in *Melophagus* they differ from those found in the higher Muscoidea, where the corpus allatum is a single median unpaired structure in the larva (the

"ring gland" or "Weismann's ring," surrounding the aorta), as well as in the adult. In *Lucilia sericata*, the corpus allatum is very inconspicuous in the larva, increasing in size in the pupa and the adult. Whether these and other differences are merely functional and correlated with those of the reproductive processes, or whether they may have some deeper, evolutionary significance, is open to question. It will be necessary to study first the incretory glands in other, more generalized Hippoboscidae and in the pupiparous, free-living tsetse-flies. The true function of the corpora allata in insects is as yet obscure; although there is some evidence that, in *Calliphora*, *Drosophila*, and *Musca*, the larval ring gland is the source of the hormone which induces the formation of the puparium.

VII. Respiratory System. The only complete account of the tracheal system of a hippoboscid is that of *Melophagus ovinus*, recently published by Webb (1945), from which the following is condensed (Figs. 16A-D). The system comprises two main dorsal *longitudinal tracheae* extending forward from the posterior end of the abdomen into the thorax, where they open into a series of air sacs, and of a subsidiary pair of laterally disposed *spiracular tracheae* connecting the abdominal spiracles of one side with each other and with the dorsal longitudinal trachea. It is identical for both sexes in the head and thorax, but shows some slight sexual modifications in the abdomen, as was first noted by Massonat (1909, p. 175).

There are two pairs of *thoracic air sacs*. The large *anterior* pair (*ATA*) occupy the greater part of the thorax and the *prothoracic spiracles* (*POS*) open directly into their anterolateral angles. They join anteriorly to form a short median trunk entering the head, where it gives rise to four branches further subdivided for the tracheation of the head. Three pairs of tracheae pass directly from the anterior sacs to the respective pairs of legs. The *metathoracic spiracles* (*MES*) open directly into the posterolateral angles of the anterior sacs, dorsal to the tracheae of the hind legs. The very small *posterior thoracic air sacs* (*PTA*) extend upward to the dorsal surface of the thorax and are joined basally by means of a short tracheal trunk to the anterior thoracic air sacs. The two dorsal longitudinal tracheae of the abdomen, upon entering the thorax, open into the posterior thoracic air sacs and pass on to join the anterior thoracic air sacs at the level of the mid legs.

In the abdomen of the male (Fig. 16B), the two *dorsal longitudinal tracheae* (*DLT*) arise from the 6th pair of abdominal

spiracles (*SP6*) and pass forward on either side to join the thoracic air sacs. A *dorsal commissure* (*TDC*) usually connects both longitudinal tracheae. Immediately after leaving their point of origin, each dorsal trachea bifurcates and forms two trunks running side by side. These reunite at the level of the 4th abdominal spiracle (*SP4*) and continue forward as a single trachea receiving in turn a branch from each of the first five abdominal spiracles (*SP1* to *SP5*). Each of the two subsidiary *spiracular tracheae* (*SPT*) arises from the 7th abdominal spiracle (*SP7*), bifurcates almost immediately, runs beneath the double dorsal longitudinal trachea and reunites just behind the level of the 4th abdominal spiracle. It then diverges into a lateral position, receives branches from the first five abdominal spiracles and finally joins the dorsal longitudinal trachea near the level of the 1st abdominal spiracle. A *branch* (*TVM*) arises from the 1st abdominal spiracle of each side, running downward and backward to supply the ventral muscles. The passage of air from the thoracic air sacs to the abdominal tracheal system is largely controlled by an intra-tracheal valve (at *INV*), inside the anterior region of each of the dorsal longitudinal tracheae. The valve consists of a flat sclerotized sheet attached to the floor of the trachea at the point of entry of the branch from the 2nd abdominal spiracle and extending forward as a horizontal lamina almost to the base of the posterior thoracic air sac. This structure allows air to pass freely from the longitudinal trachea to the thoracic air sacs, but will cut off most of the flow of air in a reverse direction.

The abdominal tracheal system of the female (Fig. 16A) differs from that of the male mainly as follows. The subdivision of the two *dorsal longitudinal* (*DLT*) and the two *spiracular tracheae* (*SPT*) in the posterior half of the abdomen is greatly increased, and an anastomosing mass of large *tracheal trunks* (*TAN*) is formed lying one above the other on either side of the posterior dorso-ventral muscles. The 1st abdominal spiracle (*SP1*) remains connected with the dorsal longitudinal trachea, but is severed from the spiracular trachea. The branch from each of the 1st abdominal spiracles, which in the male supplies the dorsal muscles (*TVM*), breaks up into a larger mass of tracheoles now associated with the anterior region of the uterus. In addition, a similar branch arising from the spiracular trunk midway between the 2nd and 3rd abdominal spiracles, and a third, somewhat smaller branch, from the 7th spiracle, supply the lateral and posterior regions of the uterus respectively.

All Hippoboscidae have two pairs of *thoracic* and seven pairs of *abdominal spiracles*. Keilin (1944) has shown that the anterior pair of thoracic spiracles are *prothoracic* (*POS*), not mesothoracic as had been supposed, since they are placed in the first thoracic segment of the dipterous larvae. The posterior pair are *metathoracic* (*MES*), being placed in the third thoracic segment. The location of the seven pairs of abdominal spiracles (*SP1* to *SP7*) was discussed in connection with the morphology of the abdomen.

In *Melophagus ovinus*, the prothoracic spiracles are larger than any others and situated mostly dorsally on the antero-lateral surface, above and slightly behind the fore coxae. According to Webb (1945a), the *external aperture* (*EAP*) is almost circular and opens immediately into a cylindrical atrium (Fig. 16D). The walls of the *atrium* (*AT*) are beset with upwardly curving, chitinous spines. At the proximal end of the spiracle, the walls are turned inward to form a stout, sclerotized ledge surrounding the elliptical *internal aperture* (*IAP*), which may be closed by a *diaphragm* (*DM*). The diaphragm is composed of two folds of soft chitin lying on either side of the internal aperture and rigidly fixed to the lower surface of the stout ledge of the inner aperture. An *occluser muscle* (*MOC*) passes from the anterior edge of the diaphragm to an *apodeme* (*APO*) arising from the inner surface of the thorax. The contraction of this muscle stretches the diaphragm longitudinally, approximates the two lips and closes the inner aperture. When the occluser muscle relaxes, the diaphragm returns to the open position by the elasticity of two sclerotized bars (*cba*), situated in the diaphragm on either side of the aperture. The smaller metathoracic spiracles are placed in the furrow between the thorax and abdomen, facing posteriorly. In structure they differ from the prothoracic spiracles only in minor details (Fig. 16C).

The abdominal spiracles differ greatly from those of the thorax, but are alike in all seven pairs. The atrium comprises three successive, intercommunicating chambers, with smooth inner walls; the outermost chamber is the largest and opens by a circular aperture; the second and third are rather short and partially invaginated into the first. The innermost chamber communicates with the trachea by a short, narrow, thickly sclerotized tube, inserted into the side of which is a stout sclerotized rod upturned at its distal end to form two alate processes at right angles to the shaft. From the inner surfaces of these processes an occluser muscle passes forward and embraces the sclerotized tube on which it becomes inserted. The contraction of this muscle operates on the sclerotized rod constrict-

ing the channel in the sclerotized tube. Below the insertion of the rod, the connecting tube widens slightly before entering the trachea and is here lined with long hairs.

From an analysis of the structure of the respiratory system and experiments on the rate of entry of ground derris dust, Webb (1945*a*; 1945*b*) concluded that mechanical ventilation of the tracheae normally takes place in *M. ovinus* and results from pumping movements of the abdomen. Contraction of the abdomen compresses the abdominal tracheae and forces the air they contain over the intra-tracheal valves into the thoracic air sacs, where a slight positive air pressure is then maintained. This pressure is held on the one hand by the closed diaphragm of the thoracic spiracles, and on the other by the intra-tracheal valves which prevent the return of air into the abdominal tracheae. When the muscles relax and the abdomen expands, the abdominal tracheae resume their normal shape and air is drawn in through the abdominal spiracles. When this process has been completed, the diaphragms of the thoracic spiracles open and the positive pressure in the air sacs is released. The diaphragms close before the next contraction of the abdomen.

Prior to Webb's work, the respiratory apparatus of *Melophagus ovinus* had been partially and mostly incorrectly described by Lyonet (1829; 1832), Dufour (1831; 1844; 1845; 1851), Krancher (1881), Massonat (1909), and Hassan (1944). There are also a few data on the respiratory system of *Hippobosca* by Dufour (1825; 1831; 1844; 1845; 1851) and Massonat (1909), of *Ornithomyia* by Dufour (1831; 1844; 1845; 1851), of *Pseudolynchia* by Massonat (1909), and of *Crataerina* by Krancher (1881) and Massonat (1909). All these accounts are too fragmentary for an intelligent comparison with *Melophagus*. Massonat was inclined to believe that the respiratory system was more important in the apterous and subapterous than in the fully-winged forms.

VIII. Circulatory System. The blood of the Hippoboscidae consists of the usual haemolymph carrying a few suspended cells or haemocytes. A qualitative and quantitative investigation of its organic and inorganic constituents has not been undertaken.

The haemolymph is colorless in most species; but in some *Ornithomyiinae* of birds it contains a pale-green coloring matter, visible through the lighter areas of the integument. The occurrence of this color in certain bird-flies was discussed before. Kemper (1951, pp. 232-234) studied it more carefully in *Crataerina pallida*. It would seem that it appears in flies only after they have fed: at first the imbibed red blood shows distinctly through the integument

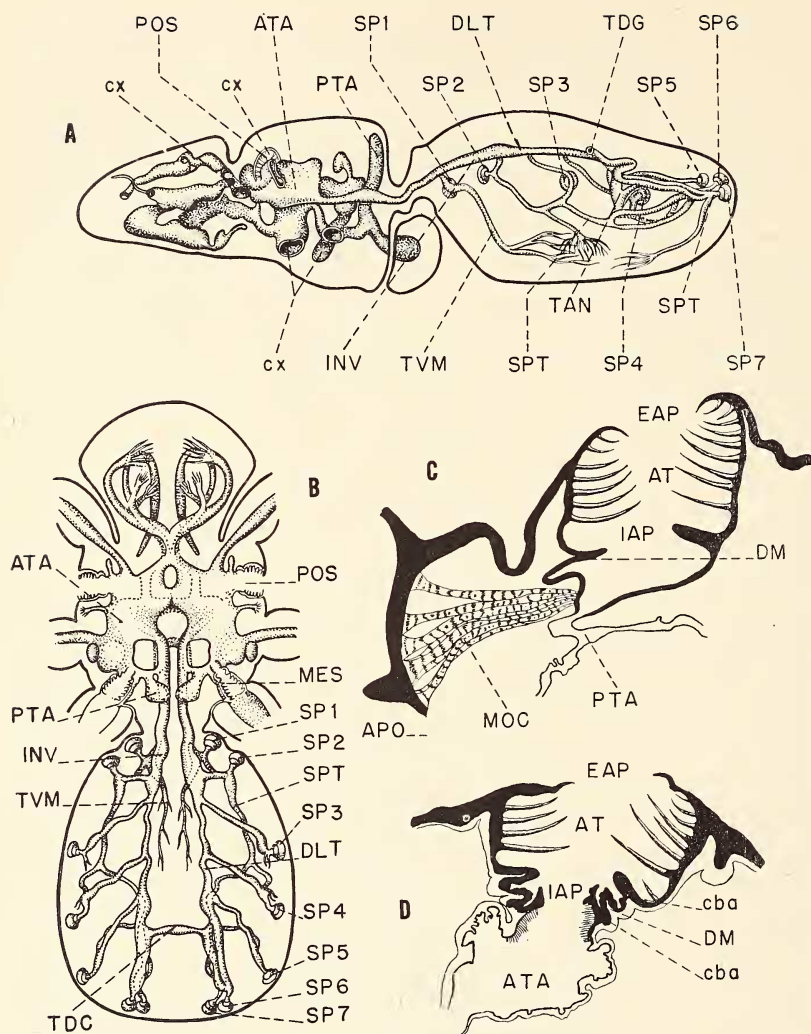


FIG. 16. *Melophagus ovinus* (Linnaeus); respiratory system; modified after Webb (1945a). **A**, tracheal system of female in profile from the mesial aspect; **B**, tracheal system of male from the dorsal aspect; **C**, longitudinal section of metathoracic spiracle; **D**, longitudinal section of prothoracic spiracle, **APO**, apodeme; **AT**, atrium; **ATA**, anterior thoracic air sac; **cba**, sclerotized bars of diaphragm; **cx**, sectioned connections with left thoracic air sacs; **DLT**, dorsal longitudinal tracheae of abdomen; **DM**, diaphragm; **EAP**, external aperture of spiracle; **IAP**, internal aperture of spiracle; **INV**, location of intratracheal valve; **MES**, metathoracic spiracle; **MOC**, occlusor muscle of spiracle; **POS**, prothoracic spiracle; **PTA**, posterior thoracic air sac; **SP1**,

of the anterior part of the abdomen, while the caudal half is at least partly deep bluish-green; one or two days later, the anterior portion of the abdomen also turns deep-green. The changes are somewhat more pronounced in the male than in the female. Kemper quotes unpublished work of H. Remmer, showing that the green color of *Crataerina* is a degradation product of the red haemoglobin of the host's blood, a so-called "verdoglobin." Normally the green color passes later in the general body cavity, first in the hind legs, spreads then to the other legs and the soft parts of the head near the proboscis, and sometimes enters the base of the wings and certain areas of the thorax. It was observed twice that a half-grown larva voided prematurely by a greenish female was likewise tinged with green. It is doubtful whether the dull-green color of the Hippoboscidae is due to the same chemical substance as that found in some other Diptera, such as certain Stratiomyidae and Tabanidae. Ad. Lutz (1912, pp. 79-81) showed that the green color of certain American tabanids (*Tabanus limpidapex*, *T. mexicanus*, and others) also resides in the haemolymph, as shown by the blood currents following the pulsations of the heart. He states that the green tinge of these flies is a constant feature of the species and not the result of a previous blood meal. That its occurrence in tabanids is independent from the blood diet is further shown by its presence in both sexes, though the males of these flies never bite. A comparison of the chemical properties and origin of the green coloring matter of the blood in the Hippoboscidae and Tabanidae might be of unusual interest.

In *Hippobosca equina* the main blood vessel, or *heart*, lies dorsally on the middle line of the abdomen, immediately beneath the exoskeleton. It is a muscular tube comprising five chambers, each opening by a pair of lateral *ostia*, but without inner dividing septa. The anterior prolongation of the heart into the thorax, or *aorta*, is much narrower, simple and without lateral ostia. The heart is contained in a *pericardial cavity* (or dorsal sinus) separated from the body cavity below by the pericardial or dorsal diaphragm; on either side it is joined by the branches of five wing-like muscles and many tracheal ramifications. The remainder of the pericardial cavity is filled with peculiar *pericardial cells* (or nephrocytes), which appear to have an important excretory function. According to Hase (1927,

SP2, *SP3*, *SP4*, *SP5*, *SP6*, *SP7*, first, second, third, fourth, fifth, sixth and seventh abdominal spiracles; *SPT*, longitudinal spiracular tracheae; *TDC*, dorsal commissure, sectioned at the connection with the left half of the tracheal system in Fig. A; *TVM*, tracheal branch from 1st abdominal spiracle.

pp. 205-211), the rate of beat of the heart varies greatly in *Hippobosca equina* (from 60 to 200 pulsations per minute) and the beat is interrupted now and then by pauses. It also changes continually in response to outside and inner factors.

As in many other insects, circulation in the appendages is controlled or activated by accessory pulsating organs. Hase (1927) found such organs in *Hippobosca equina* on the legs, one in each tibia, its pulsations being observed at the soft membranous joint between femur and tibia, on the under (or inner) side of the base of the tibia. In the wing an accessory heart occurs at the extreme base of the second basal cell, where the elbow-shaped common origin of the 4th and 5th longitudinals is thickened and discolored. It is interesting that the accessory hearts of legs and wings do not always pulsate in unison with the main abdominal heart and that the rate of beat is not always the same in all legs. Circulation in the wings is probably similar to that observed in some Muscoidea, where the blood enters from the thorax by the costa and adjacent anterior veins and returns to the body by the posterior veins (Thomsen, 1938, p. 419, fig. 1, showing the direction of the blood stream in the wing of *Musca domestica*).

The only published studies of the circulatory system of the Hippoboscidae seem to be those by Massonat (1909) and Hase (1927) for *Hippobosca*. Schuurmans Stekhoven and his co-workers will publish shortly observations on the circulation in *Pseudolynchia canariensis*.

IX. Reproductive System. The peculiar reproductive organs are an outstanding characteristic of the Hippoboscidae.

A. Internal Male Organs. In *Melophagus* (Fig. 17A) and *Hippobosca*, the pair of *testes* (*T*) are simple, slender tubes of considerable length (in some cases 4 to 5 times the length of the body when uncoiled), each closely convoluted into an oval tangle, from which the somewhat club-shaped blind end protrudes. Each appears to be a single sperm tube, in which the male germ cells develop into spermatozoa. It continues posteriorly as a very short, slightly swollen *vas deferens* (*VD*), which opens directly (without intervening vesicula seminalis) into the single, median *ductus ejaculatorius* (*DE*). This is moderately long, slightly swollen at its origin and connected through the gonopore with the endophallic chamber of the aedeagus. The apical portion of the ductus ejaculatorius makes a loop to the left around and behind the rectum. There are two pairs of unusually long vehicular or *accessory glands* (*AG*), each pair opening by a short common duct in the correspond-

ing vas deferens at the point where the latter enters the ductus ejaculatorius. In *Ornithomyia*, according to Holmgren (1903), there are five accessory glands, the anterior pair being replaced by three glands.

The male organs of the Hippoboscidae differ greatly from those of most Muscoidea in the lack of a differentiated vesicula seminalis, in the unusual development and tubular shape of the testes and of the accessory glands, and in the apical loop of the ductus ejaculatorius around the rectum. They agree in these peculiarities with those of the Glossinidae (Fig. 18A), which, however, have only one pair of accessory glands. The male genital organs of the Nycteribiidae and Streblidae have been too little investigated for an intelligent comparison; but, in the Nycteribiidae, they appear to combine some features of the Muscoidea and of the Hippoboscidae.

B. *Internal Female Organs* (Fig. 17B). The female genital tract lies ventrally in the posterior part of the abdomen, close to the ventral body wall. In a newly-emerged fly, it is short and flattened, occupying only a relatively small part of the shrivelled abdomen. As the development of a larva progresses, the uterus increases greatly in length and thickness and eventually the genital organs fill most of the greatly expanded abdomen. A pair of ovaries (*O*), one directed to the right and the other to the left, lie dorsally to and a short distance behind the anterior or proximal extremity of the uterus (*U*). The ovaries are ovoid and strikingly dissimilar in size, because they alternate in producing a mature ovum, the outstanding feature in the reproduction of the Hippoboscidae and other Diptera with integral viviparity (so-called pupiparity). Each ovary narrows into a very short *lateral oviduct* (*LD*), which combines with its fellow to form a rather spacious, but short, common or *median oviduct* (*MD*), sharply set off from the uterus. In *Melophagus* and *Lipoptena*, the junction of the two lateral oviducts with the median oviduct forms a somewhat dilated *atrium* (*AT*; preuterus), which functions as a reservoir for the sperm. According to Graham and Taylor (1941), in *M. ovinus* sufficient sperm is thus stored from a single mating to last during the female's lifetime, which is not so surprising in view of the few larvae that are produced meanwhile. The median oviduct joins the genital chamber, or uterus (*U*), somewhat behind the latter's latero-ventral end. In the newly-emerged fly, the uterus is a broad, depressed tube, about half as long as the abdomen, attached by strong muscles to the dorsal and ventral inner surfaces of the integument; but when it contains a growing larva, it stretches considerably and eventually occupies

half or more of the cavity of the abdomen. The uterus narrows posteriorly into a short *vagina* (VA), which opens externally through a crescentic, slit-like *vulva* (VU) at the postero-ventral end of the abdomen (behind the anus), between two genital plates. The foregoing arrangement of the parts is that of *Melophagus ovinus*, as described by Pratt (1899) and others. The few other genera examined thus far differ only in minor details. According to Hardenberg (1927; 1929), *Lipoptena* is very similar; but the atrium lies to the right of the uterus (not dorsally on it, as in *Melophagus*) and the left lateral oviduct is much longer than that on the right side. He also states that in *Hippobosca variegata* (= *H. maculata*), *H. equina*, *H. rufipes*, *Crataerina pallida*, and *Stenepteryx hirundinis*, there is no atrium, the two lateral oviducts opening directly in the median oviduct, while the latter is not sharply set off from the proximal end of the uterus.

The dorsal anterior (or proximal) end of the uterus receives two sets of *glands*. In *Melophagus ovinus*, where there are two pairs, the glands of each pair first combine in a common duct and these two ducts then unite in a single very short duct opening in the uterus. The hind pair are two large, extensively branched, tubular structures, evidently modified *accessory* (or fecundatory) *glands*. They have acquired a nursing function seemingly in all Hippoboscidae, secreting a milk-like fluid on which the larva feeds, so that they can properly be called *milk-glands* (MG). The *forward glands* (FG) vary in number, size, structure and function in the family. Their homology has been disputed; but there is now little doubt that they are modified spermathecae (receptacula seminis), since they occupy the same position and open at the same point of the uterus as the functional spermathecae of the higher Muscoidea (such as *Glossina*, Fig. 18B). In *Crataerina pallida* and *Stenepteryx hirundinis*, according to Hardenberg (1927; 1929), there are three such glands (a frequent number in the Muscoidea, though *Glossina* has two only), which are short, unbranched and actually function for the storage of the spermatozoa after mating. The same author describes the forward glands of *Hippobosca* as long and branched (also observed by Dufour, 1845, p. 92; pl. 3, fig. 35, *H. equina*); he found three of them in *H. rufipes*, but only a pair in *H. variegata* (= *H. maculata*) and *H. equina*; he also states that they no longer function as spermathecae, the spermatozoa being stored instead in the oviducts, since there is no atrium. Hardenberg suggests no other function for the branched forward glands of *Hippobosca*; I surmise that they serve to some extent as milk-glands. In *Melopha-*

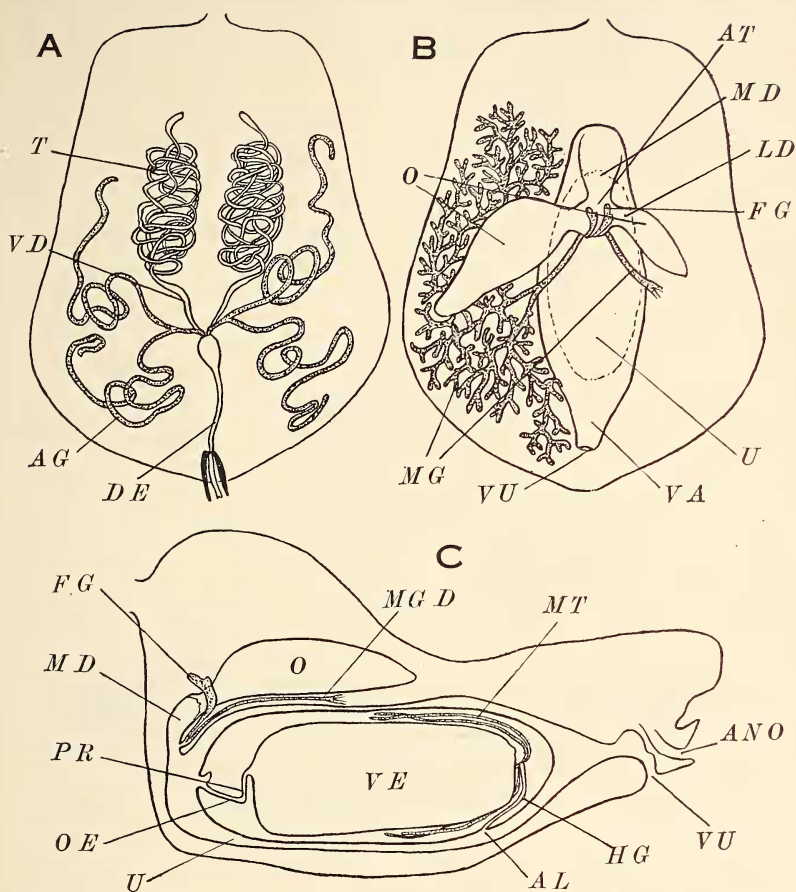


FIG. 17. *Mclophagus ovinus* (Linnaeus). **A**, male organs: AG, accessory glands; DE, ductus ejaculatorius; T, testes; VD, vas deferens. **B**, female organs from above: AT, atrium; FG, forward pair of glands; LD, lateral oviduct; MD, median oviduct; MG, milk glands (drawn on one side only); O, ovary; U, uterus; VA, vagina; VU, vulva. **C**, longitudinal section of female abdomen and of larva developing in uterus: ANO, anus of adult; AL, anus of larva; FG, forward gland; HG, hind gut of larva; MD, median oviduct; MGD, duct of milk-gland; MT, Malpighian tubules of larva; O, ovary; OE, oesophagus of larva; PR, proventriculus of larva; U, uterus; VE, ventriculus of larva; VU, vulva. All modified after Pratt, Roubaud and others.

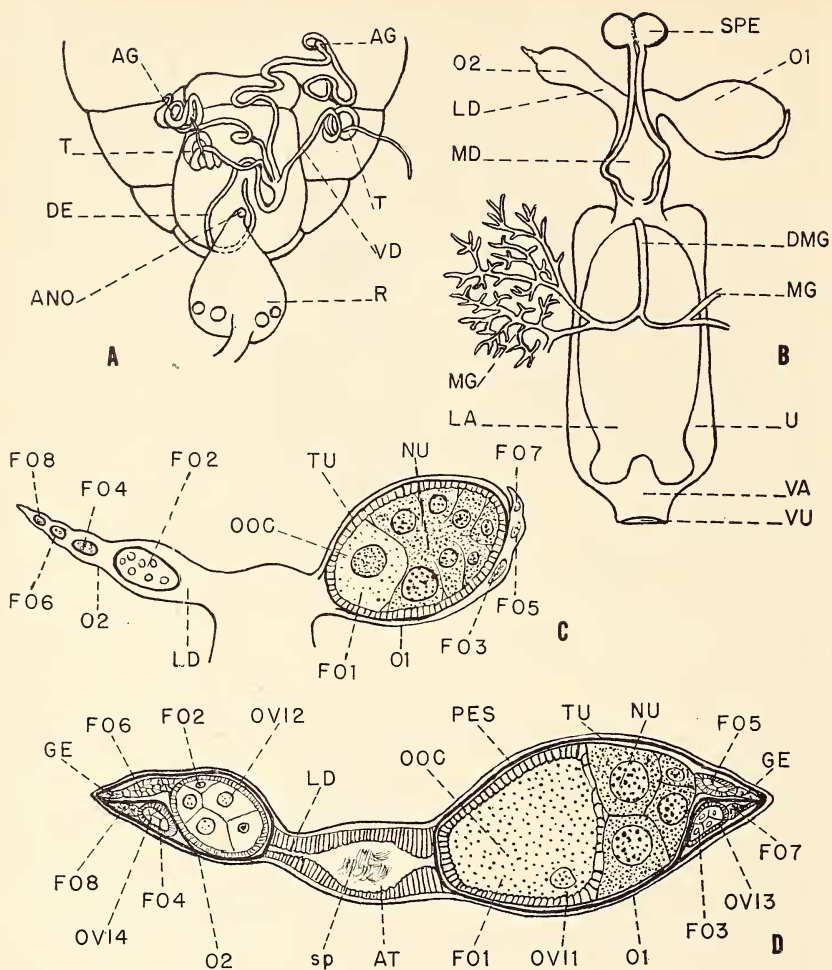


FIG. 18. **A-C**, *Glossina palpalis* (Robineau-Desvoidy). **A**, male genital organs, modified after Minchin (1905, *Proc. Roy. Soc. London, B*, 76, p. 542, fig. 5). **B**, female genital organs, modified after Roubaud (1909, p. 430, fig. 91) and Newstead (1924, p. 5, fig. 1). **C**, inner structure of ovaries, modified after Newstead (1909) and Hagan (1951). **D**, *Melophagus ovinus* (Linnaeus); inner structure of ovaries, modified after Pratt (1899). AG, accessory glands; ANO, anus; AT, atrium; DE, ductus ejaculatorius; DMG, common duct of milk glands; F01, F02, F03, F04, F05, F06, F07, F08, follicles in the order in which they produce ova; GE, germarium; LD, lateral oviducts; MD, median oviduct; MG, milk glands; NU, nurse cells; O1, O2, right and left ovaries; OOC, oöcyte; OV11, OV12, OV13, OV14, ovarioles in the order in which they produce ova; PES, peritoneal sheath; R, rectum; sp, sperm; SPE, spermathecae; T, testes; TU, tunica propria of each ovariole; U, uterus; VA, vagina; VU, vulva.

gus and *Lipoptena*, however, they are reduced to a pair of short, thick, simple tubes, which do not store spermatozoa and may be rudimentary and functionless. Zacharias (1928, p. 685) observed that in *M. ovinus* the forward glands occasionally contain some spermatozoa, which he believes are resorbed there.

Each of the two ovaries is encased in a peritoneal sheath of unusual thickness, forming an elastic sac. In *Melophagus ovinus* (Fig. 18D), the only hippoboscid in which the inner structure has been completely described (Pratt, 1899), each ovary contains two ovarioles (*OVI*), each enclosed in its own *tunica propria* (*TU*), and each with a *germarium* (*GE*) at the bottom end, followed by two successive follicles (*FO*). In each ovary also, the two ovarioles function alternately, so that the ovary contains only one developing ovum (*OV*) at any time. Hardenberg states that the ovaries of *Lipoptena*, *Hippobosca*, *Crataerina*, and *Stenepteryx* agree with those of *Melophagus*; unfortunately he describes the inner structure of none of these genera.

A comparison with the female genital tract of *Glossina* (Fig. 18B) discloses that its structure is fundamentally the same in the Hippoboscidae and the Glossinidae, and is, moreover, essentially that of the other higher Muscoidea. *Glossina* differs in the following particulars, according to Roubaud (1909, p. 430, fig. 91), Newstead (1924, p. 5, fig. 1), and Hagan (1951, pp. 112–118), the differences being all seemingly of minor importance. (1) Each ovary comprises only a single ovariole, instead of two. (2) The single ovariole contains four or five follicles at a time, instead of two, so that the total number of follicles in each ovary is about the same. The two foregoing differences are based on the assumption that Pratt's interpretation of the inner structure of the ovary of *Melophagus* is correct and that the other genera of Hippoboscidae agree with this. Personally I feel that the matter calls for further investigation. Whether the ovaries of *Glossina* open directly in the common oviduct or by means of intervening lateral oviducts, seems to be a matter of definition. In *Melophagus* and *Lipoptena*, an atrium intervenes to differentiate more clearly the lateral oviducts from the median oviduct; but in other Hippoboscidae, which lack the atrium, I can see little difference from the arrangement of *Glossina*. (3) The two ducts of the accessory or milk-glands unite into a long common duct before opening in the uterus. (4) The two fully functional spermathecae are globular, firmly united by a transparent tunica propria, but each with its own long, slender tube connecting it with the uterus; in the Hippoboscidae they are clearly degenerated, func-

tionless in some genera, or possibly with a secondarily acquired nutritive function in others. From what little is known of the female genital tract of the Nycteribiidae and Streblidae, these insects differ mainly in the lack of a differentiated oviduct, the two ovaries opening directly in the uterus, in the presence of a pair of short, simple, functional spermathecae, and in the more elongated common duct of the two ramified milk-glands. It may also be noted that while the maturing ovum of *Glossina* contains 15 nurse cells in addition to the oöcyte (as in most Muscoidea), only 7 nurse cells are present in the Hippoboscidae (at any rate in *Melophagus ovinus*, the only species examined in this respect). According to Hardenberg (1927; 1929), the Nycteribiidae have 7 nurse cells (in *Cyclopodia*) and the Streblidae 15 (in *Nycteribosca*).⁴

The reproductive system of *Melophagus* was studied repeatedly during the past century, beginning with v. Siebold (1837) and Dufour (1844; 1845; 1851); Leuckart (1854; 1855; 1858) was the first to interpret it correctly and he was followed by Pratt (1899), Berlese (1899), Holmgren (1903), Roubaud (1909), Patton and Cragg (1913), Hardenberg (1927; 1929), Zacharias (1928), and Zavattari (1928). It was described by Réaumur (1742), Dufour (1825; 1844; 1845; 1851), Massonat (1909), Patton and Cragg (1913), Hardenberg (1927; 1929), and Zavattari (1928) for *Hippobosca*; by Hardenberg (1927; 1929) for *Lipoptena*; by Dufour (1844; 1845; 1851) and Holmgren (1903) for *Ornithomyia*; by Hardenberg (1927; 1929) for *Crataerina*; by Hardenberg (1927; 1929) and Huzimatu (1938) for *Stenepteryx*. Hagan (1951, pp. 159-169) discussed the female genital tract of the Hippoboscidae from the literature and compared it with that of the Glossinidae.

DEVELOPMENT AND EARLY STAGES

Together with other so-called "pupiparous Diptera" (Nycteribiidae, Streblidae and Glossinidae), the Hippoboscidae are endowed with integral *viviparity* of a peculiar, *adenotrophic* or incubating type (H. R. Hagan, 1948, p. 64; 1951, p. 59; formerly called by him, 1931, p. 22, *intussuctio-viviparity*), not known at present among other insects. In these flies the egg contains sufficient yolk to nour-

⁴ In the text of his paper Hardenberg (1927, p. 36; 1929, p. 532) states definitely that *Cyclopodia ferrarii* (cited by error as *C. plen-octena* in 1927) has 7 nurse cells, like the Hippoboscidae; but in the summary (1927, p. 42; 1929, p. 538) he attributes 15 nurse cells to both the Nycteribiidae and the Streblidae.

ish the embryo until the first instar larva hatches, after which specialized maternal organs feed the offspring in the uterus throughout larval life.

In the Hippoboscidae (Fig. 18D), each of the two follicles of each of the two ovarioles contains a developing ovum; so that at any one time the ovary shows at most four developing ova, or a total of eight for both ovaries of a fly. Normally the two ovaries alternate in producing a mature ovum and so do the two ovarioles in each ovary. One of the ova develops therefore far ahead of the other seven, so that the two ovaries are strongly asymmetrical in size. When fully mature, the ovum moves by way of the oviduct to the uterus, where it eventually hatches into a first instar maggot. Another ovum now matures in one of the ovarioles of the ovary on the opposite side; it does not move to the atrium until the preceding larva is fully developed and has been voided by the fly. After an ovum has left an ovariole, the germarium produces a new follicle, thus restoring the original number of eight ova. The ovaries thus engender a series of mature ova, one after another, until the productivity of the germarium is exhausted or the fly dies. As a consequence, the total number of ova produced by a female is very small as compared with the numerous offspring of most other insects. According to Dr. Hagan (*in litt.*, 1951): "Oöcyte formation probably follows that of related Diptera; therefore, in the *germarium* (GE), a cell from the germal mass, at intervals, undergoes 3 divisions, thus producing 8 daughter cells. Of these, one will be oöcyte (OOC), the remaining 7 cells will be *nurse cells* (NU). This process does not subtract 8 cells from the reserve in the germarium with each ovulation, but only one. The original supply then would seem more than ample to last the entire life of the female." Lassmann (1936, p. 398) found on two occasions in *Melophagus ovinus* that the uterus contained two eggs, both with complete egg envelopes and micropyles. As he never found twin larvae in the uterus he assumed that one of the larvae is aborted as soon as it hatches or succumbs due to lack of nourishment.⁵

Egg. Upon leaving the ovary, the mature egg is typically muscoid, about 1.16 mm. long and 0.3 mm. wide, elongate cylindrical, tapering at the poles and blunter posteriorly, very slightly concave dorsally and somewhat convex ventrally. It is enclosed in a

⁵ Abnormal voiding of twin larvae has been observed on rare occasions in the tsetse-fly, *Glossina palpalis*. It is therefore not impossible that it might sometimes occur in the Hippoboscidae.

membranous two-layered chorion, at the cephalic end with a funnel-shaped depression, in which the pores of the micropyles open. The depression is soon filled with spermatozoa, impregnation occurring either in the atrium or in the oviduct. The embryonic development was rather fully investigated in *Melophagus ovinus* by Leuckart (1858), Pratt (1893; 1897; 1900), Hardenberg (1927; 1929), and Lassmann (1936); their observations have recently been critically reviewed by Hagan (1951, pp. 169-186), to whom the reader is referred for the details. Hardenberg (1927; 1929) also published fragmentary observations on the gastrulation of *Lipoptena cervi*, *Stenepteryx hirundinis*, and *Crataerina pallida*.

The maturation processes of the egg were partly described for *M. ovinus* by Lassmann, but actual fertilization was not observed. Polyspermy seems to be the rule in *Melophagus*, each egg containing six sperms in the early maturation stages.

According to Cooper (1941), in *Melophagus ovinus* both male and female gonial plates show a diploid set of 18 chromosomes, the largest number yet reported in the Diptera Cyclorrhapha. Lassmann's earlier observation of only 8 haploid somatic chromosomes in the oöcyte of the sheep- ked was erroneous. On the other hand, Cooper (1942; 1944a) found that the diploid set of male *Olfersia bisulcata*, as determined from spermatogonia and spermatocytes, has only 8 chromosomes. I am under obligation to Dr. K. W. Cooper for calling my attention to several other features of chromosomal behavior in these flies. In both acalyptrate and calyptrate Muscoidea, no cases are known of a regular occurrence of chiasmata connecting the pairing chromosomes at meiosis in the male and in this respect the meiosis of *Olfersia* and *Melophagus* is like that of other Muscoidea. In first spermatocytes the sex chromosomes of the Muscoidea have only a small point of association in pairing and this is also true of *Olfersia*; but in *Melophagus* the sex chromosomes do not pair at all and their mode of segregation is of a peculiar type. Furthermore, in both *Olfersia* and *Melophagus*, at meiosis in the male the autosomes, like the sex chromosomes of most muscoid flies, pair only by small segments; in this regional localization of meiotic conjunction in the autosomes of males, they differ from the Muscoidea (as well as from the Streblidae and Nycteribiidae investigated thus far), in which the autosomes pair along sizeable lengths so far as known.

Larval Instars. The following account refers to *Melophagus ovinus*, the larva of which is best known. The first larval instar, hatching from the egg, is more or less maggot-like, with superficial

traces of segmentation (12 segments according to Leuckart), 8 pairs of rudimentary lateral spiracles, a posterior anal opening, and anteriorly a small, nipple-like projection bearing the mouth between two minute lateral papillae. There is no trace at this stage of a cephaloskeleton nor of mouth hooks. A posterior stigmatic plate, at the distal end, bears a single pair of stigmata. After the first moult, the maggot-like shape disappears, the second larval instar being a plump ellipsoid. In the course of intra-uterine development there are two moults in all, between the three larval instars. The first moult occurs soon after the egg hatches and the second when the second instar is about 2.7 mm. long.

The third larval instar is barrel-shaped, slightly flattened at both ends and ventrally, 3.5 to 3.7 mm. long, about 1.9 mm. wide and about 1.6 mm. thick, when fully grown. The mouth is directed cephalad in the female's body, facing the median oviduct. The posterior end, with the anus and respiratory openings, faces the vulva. The larva (Fig. 17C) lies free, without connection with the mother's tissues and separated from the inner wall of the uterus by the exuviae of the earlier instars. The only external traces of segmentation are two curved rows, one on each side both dorsally and ventrally, of 7 shallow depressions (mistaken for spiracles by Bonnet, 1776) marking the insertions of dorso-ventral respiratory muscles which run on either side of the digestive tract. These are the only cutaneous muscles developed in the larva. Anteriorly the integument shows the first indications of the circular and semicircular seams or weakened lines, typical of all *Cyclorrhapha*, along which the puparium will break open for the escape of the adult. According to Pratt, the first and second larval instars of *Melophagus* show no traces of these seams, which appear only after the second larval moult.

A tubular heart extends nearly the whole length of the body, dorsad of the mid-gut. Adipose tissue is unusually abundant in the general cavity (Oektay, 1951) and the first indications of the sexual organs may be traced. The nervous system is similar to that of the muscoid maggots, but the several ganglia are less concentrated in a central mass. There appear to be no sense organs.

The respiratory system of the third larval instar is metapneustic, on the whole normally developed, although showing some unusual features correlated with intra-uterine life. There are two main longitudinal, dorsal tracheal trunks, with several transverse connectives and many side branches ramifying throughout the body. Of the eight pairs of rudimentary lateral spiracles of the first stage

larva, the six hind pairs are completely lost; the two anterior pairs, prothoracic and metathoracic, persist as microscopic, functionless apertures of the cuticle, just before the circular seam and above the horizontal seam. The main tracheal trunks do not open anteriorly and posteriorly, as in most Muscoidea, but only in a pair of highly modified distal stigmal plates, the "*polypneustic lobes*" of Newstead (1918). In *Melophagus* each of these lobes is furnished with a deep, cup-shaped pit, near the bottom of which and occupying a sub-central position is the stigmal opening which communicates directly with one of the main tracheal trunks; near the rim or periphery of the pit are two large stigmata: one toward the venter, the other toward the dorsum; in addition there is also a very minute pore-like stigma; and outside the pit an outer-lateral stigma rendered most conspicuous by its large and strongly sclerotized peritreme. All the stigmata, with the possible exception of the very minute one, are connected by a thick-walled air sac or trunk, which latter can be easily traced through the integument. The stigmal plates of the larva of *Melophagus* were also studied by Keilin (1944, p. 55, fig. 48a). Buxton (1924) and Ferris and Cole (1922) state that, in the larva of *Lipoptena*, each polypneustic lobe bears three curved lines of spiracular pores, those of each line opening in a tracheal branch, the three tracheal branches uniting in a spherical chamber from which starts the rather thick-walled main tracheal trunk. A variation of this arrangement was described and figured by Ferris (1923) for *Ornithoctona fusciventris* (= *O. strigilecula*). As Buxton suggested for *Lipoptena*, the three groups of spiracular pits are evidently derived from the three slits in the anal stigmal plates of the third stage maggot of many Muscoidea. The more aberrant arrangements of *Melophagus* and other genera are further specializations. Exchange of respiratory gases is exclusively through the genital opening and vulva of the mother.

The digestive tract is voluminous. The functional mouth, opening through a conical papilla, leads to an irregular cavity, followed by the invaginated true cephalic segment (*cephalic pouch*), which is moved by a set of muscles in rhythmic contractions, so that it acts as a sucking pump to take up the liquid food. On each side of the buccal papilla, dorsally to the horizontal arch seam, there is a small papilla. The cephalic pouch contains the *pharynx* and its walls are sclerotized into a "pharyngeal skeleton" or "bucco-pharyngeal armature," as in other Cyclorrhapha. However, according to Keilin (1916, p. 401), the armature is reduced to the innermost, basal or pharyngeal sclerite, the ventral wall of which

is smooth, the distal pieces and particularly the mouth hooks being absent.⁶ There are also no salivary glands. The cephalic pouch continues in the tubular, horizontal *oesophagus* (*OE*), which bends upward abruptly into a tubular, vertical *proventriculus* (*PR*), itself opening in the very large, balloon-shaped *ventriculus* (*VE*), closed behind, which fills most of the body cavity. The *hind-gut* (*HG*) is a short narrow tube, blind anteriorly where it receives four *Malpighian tubules* (*MT*; 2 ventral and 2 dorsal), and ending in a ventrally placed *anus* (*AL*).

The peculiar structure of the digestive tract of the hippoboscoid larva is almost duplicated by that of the larval tsetse-flies. In both cases it is clearly conditioned by the intra-uterine feeding with the highly nutritious and directly assimilable secretion of the mother's milk-glands, which has induced profound changes in the physiology of digestion and absorption. According to Roubaud (1919), in the tsetse-flies, the food received in the ventriculus of the larva undergoes no further digestive changes, but only a selective absorption. The epithelial cells remove mainly the adipose parts of the food to the larval body cavity. Nearly all the proteins remain unchanged inside the ventriculus and become available to the general metabolism only during the pupal stage. The continued accumulation of proteins in the ventriculus throughout larval life accounts for the enormous size of this portion of the digestive tract. There is also very little formation of nitrogenous waste products, thus making their steady elimination from the body unnecessary, which explains why the ventriculus is closed off from the hind-gut. The peculiar digestive processes of the larvae of the pupiparous Diptera no doubt have also far-reaching effects upon other phenomena in the life of these flies, such as the histological changes during pupation, the duration of pupal development, the resistance of the puparia to adverse conditions, and consequently the rate of reproduction, as may be seen by referring to Roubaud's work. In *Melophagus ovinus*, the fat entering the body cavity of the larva is stored in the adipose tissue, which, according to Oektay (1951), differs from that of the adult fly; it forms irregular lobes of one to three layers of cells and there are also isolated fat cells; it is therefore more of the usual type found in most insects.

⁶ Keilin states that he examined the larvae of *Melophagus ovinus* and *Hippobosca equina*, but unfortunately does not describe nor figure their buccal armature. He gives a figure only of the pharyngeal armature of *Glossina* and infers that in *Melophagus* and *Hippobosca* it is similar.

The nature of the larval food is of great interest. From the position of the larva in the uterus and the rhythmic movements of its cephalic pump, it should take up any material, either liquid or in suspension, that fills the common median oviduct. In *Melophagus*, Leuckart, Pratt and most other authors believe that this material is essentially, if not solely, the secretion from the milk-glands of the female. Berlese (1899), on the other hand, claims that the larva feeds on the abundant sperm and secretion from the accessory glands of the male, both being injected in the uterus at the frequent matings. Berlese also states that the secretion from the so-called milk-glands of the female has no nutritive function, but serves only to cover the newly laid larva with the sticky substance that glues the puparium to the fleece. The two views may perhaps be reconciled, as the larval food may possibly include, at least in the early larval stages, some sperm and secretion from the male accessory glands, which might explain the unusual development of the male internal organs. Zacharias (1928), however, found a few spermatozoa in the lumen of the forward pair of glands opening anteriorly in the uterus of female *Melophagus*, so that some of the superfluous sperm may perhaps be resorbed in these organs. I agree with Roubaud (1909), moreover, that the main larval food of the Hippoboscidae is the secretion from the female milk-glands. Most probably the viscose substance surrounding the freshly voided larva of *Melophagus* is also secreted by the milk-glands, as Berlese believed, since no other glands are known that might produce it. In other Hippoboscidae, however, which do not glue the puparium, but deposit clean and fairly dry larvae, the milk-glands are fully as well developed as in *Melophagus*.

Huzimatu (1938) has given a rather complete description of the three larval instars of *Stenepteryx hirundinis* (= *Lynchia nipponica* Kishida). He dwells particularly upon the tracheal system of the third instar.

Imaginal Disks. Pratt (1900, correcting his earlier papers of 1893 and 1897) found that, in *Melophagus ovinus*, the several imaginal disks, or rudiments from which the adult organs will be built up during pupation, appear at different times in the ontogeny. The cephalic and thoracic disks can be traced in the embryo, before the egg hatches. Three cephalic disks, one ventral and two dorsal, appear first, when the intestinal, tracheal and nervous systems are as yet rudimentary. The thoracic disks appear later, about the time the primitive embryonic stomodeum is involuted within a projecting papilla or sucking mouth and after the head disks are

fully formed. In all, three ventral and three dorsal pairs of disks, pro-, meso-, and metathoracic, can be traced in the embryo. It is interesting that, although adult *Melophagus* has only the merest traces of wings and lacks halteres completely, the imaginal disks of both these organs are fairly well developed and persist in the larva, as Stange (1907) also found. The abdominal disks are not developed in the embryo, but appear later, probably in the early larval instars. They were only briefly described by Pratt in his earlier paper (1897, pp. 194-197); they comprise first two pairs of anal disks, placed in a transverse row in front of the anus, which Pratt thought develop later into the sexual external appendages; seven ventral and two dorsal pairs of groups of cells, regularly distributed in the epidermis, constitute the epidermal disks; there is also a ring of imaginal epithelial cells around the anus.

Puparium. All three successive larval instars develop in the uterus of the female fly. The third instar is voided by the mother only when it is full-grown. It is practically motionless, as it lacks true muscles of progression. Once outside the mother's body it takes no food of any kind. At first it is usually dirty-yellowish or white, except for the much darker, brown or blackish posterior polypneustic lobes; the larval integument gradually turns chestnut-brown to black, while the cuticle hardens and becomes rather brittle. It thus transforms rapidly into a *puparium*, within which is formed the *true pupa*, as in all Cyclorrhapha. The soft third larval instar, in the process of being deposited, may therefore be called a *prepuparium*. In the puparium, the papillae and the closed buccal slit are barely visible at the anterior end; while posteriorly the two polypneustic lobes protrude somewhat more than in the larva. Dorsally and ventrally the two rows of 7 depressions of the larva are retained, each row placed in a slight longitudinal groove. The seams of the anterior cap, through which the adult will escape, are more or less apparent, in *Melophagus* difficult to see. The circular seam runs across and around the body (in the higher Muscoidea it is placed in the apparent maggot segment 5). The semicircular seam passes over the top to the sides, forming a bow slightly dorsad of the buccal papilla and ending in the circular seam. When about to emerge, the adult pushes blood, by contracting thorax and abdomen, into the soft-walled, reversible ptilinal pouch. The increasing pressure of the pouch on the inner wall eventually ruptures the cap at the semicircular seam into two valves, which break off at the circular seam. The opening of the

puparium by means of the ptilinum was first described by Dufour (1845, pp. 85-86) for *Melophagus ovinus*.

Because as a rule a full-grown third instar larva and not a true puparium is deposited by the female, it has been contended that the term "pupiparous" as applied to the Hippoboscidae is a misnomer. The larva when voided is, however, at least a potential puparium, since it merely needs to harden the integument. In *Stilbometopa impressa*, according to unpublished observations by Mr. I. B. Tarshis (*in litt.*, 1952), larviposition proceeds by stages: at first the larva is only partly protruded, being carried about for some time by the female, much like the oötheca of certain cockroaches; meanwhile the larval integument hardens and turns amber-colored and shiny, before the prepuparium is actually deposited. Moreover, as shown later in the discussion of pupation, in some species the larva occasionally remains in the uterus until after some of the internal pupal transformations have been initiated. In any case, the integral incubating viviparity of Hippoboscidae differs fundamentally from the partial viviparity of certain other so-called "larviparous" Diptera, which deposit larvae in an early stage of development, that feed, grow further and sometimes even moult outside the mother's body.⁷ For these reasons it would certainly be more of a misnomer and completely misleading to call the Hippoboscidae merely "larviparous." Those who wish to be unduly meticulous might perhaps use the term "larvi-pupiparous."

In all cyclorrhaphous Diptera that have been studied for the purpose, the epidermal cells become detached from the cuticle over the whole or part of the inner surface of the third larval instar, during the process of hardening into a puparium. This detached epidermis secretes a new, very thin and delicate membranous cuticle, which may be called the *prepupal* cuticle. To the inside of this sheath adhere the remains of the tracheal system of the third larval instar. Within this complete or incomplete fourth larval instar or *prepupa*, the true pupa is now formed by another

⁷ Most of the usual "larviparous" Diptera may be regarded as *ovoviviparous* (Hagan, 1951, p. 59), since the first instar larva is voided shortly after the embryo hatches from the egg. However, in cases such as the Neotropical *Mesembrinella* and *Chortinus*, the larva undergoes one or more moults in the mother's uterus and is of fair size when it is eventually deposited. Evidently it must have done a certain amount of intra-uterine feeding, so that these flies would seem to exhibit incomplete or partial adenotrophy.

moult, producing a much thicker pupal cuticle, later left behind in the puparium when the fly emerges. The production of a pre-pupal cuticle was first clearly recognized in acalyptrate Muscoidea: in *Rhagoletis* (Trypanidae) by Snodgrass (1924, *Jl. Agric. Res.*, **28**, pp. 22-23, Pl. 5, fig. C; figure reproduced by Wigglesworth, 1950, p. 58, fig. 47), in *Drosophila* (Drosophilidae) by Robertson (1936, *Jl. of Morphology*, **59**, p. 355), and in *Psila* (Psilidae) by Ashby and Wright (1946, *Trans. Ent. Soc. London*, **97**, p. 375). Its occurrence in the higher, calyptrate Muscoidea was established by Fraenkel (1938b) for *Calliphora*, *Lucilia*, *Phormia*, and *Sarcophaga*, so that it seems to be a regular feature of all Cyclorhapha. It could therefore have been anticipated in the Hippoboscidae. I was delighted to hear recently from Dr. J. H. Schuurmans Stekhoven (*in litt.*, 1952) that he observed in *Pseudolynchia canariensis* a moult within the puparium, producing a thin membrane, which generally lies very close to the thick casing; it may be visible under water, because there is often a bubble of air between the membrane and the thick cuticle of the third instar.

The true pupa at first shows externally only the abdomen and thorax, with the wings and legs well formed within their sheaths. At this stage the head lies invaginated inside the thorax. The body of the pupa shows wave-like peristaltic movements, gradually increasing in strength, until eventually one of them suddenly evaginates the head, which now becomes part of the pupa (Fraenkel, 1938a). Gäbler (1935) found on the newly formed inner pupa of *Lipoptena cervi* a pair of anterior functional spiracles (thoracic spiracular horns). In the pupa of *Melophagus ovinus*, however, according to de Meijere (1902), they form only two minute rudiments, placed rather far back of the head, scarcely projecting and appearing only as scars, without buttons or pits.

In the majority of the Hippoboscidae the outer surface of the completed and hardened puparium is bare; but in *Olfersia* it is covered with stiff, erect hairs, simple in some species, hooked in others. The bare puparia may be smooth and shiny, as in *Melophagus* and *Lipoptena*. More often the surface is engraved with a mesh of microscopic lines, though otherwise shiny, as in *Stenopteryx* and *Pseudolynchia*; sometimes it is in addition more or less punctate or minutely pitted, as in *Stilbometopa* and *Ornithesa*. In *Lynchia*, the engraved lines are deeper and form such a close network that the surface becomes alutaceous and dull. The puparium of *Hippobosca* appears dull and finely punctate under a hand lens;

but a higher magnification discloses that the "punctures" are actually raised, very short, triangular spinules.

After the adult emerges there is sometimes a certain amount of imaginal growth in the abdomen, at least of the female. The considerable increase in size after engorging and during pregnancy may be due entirely to the stretching of the folds of the integument. There may be in addition a true growth of some of the internal organs. Theodor (1928, p. 285) observed that, in *Lipoptena capreoli* (= *L. caprina*), the mid-gut of a newly emerged ked is 0.9 to 1 cm. long, but reaches 4 to 5 cm. in a ked 14 to 20 days old. Growth is restricted to the mid-gut and is due to the enlargement of existing cells of the wall, not to cell division. The milk-glands likewise grow in size after emergence.

NATURAL HISTORY

As the term implies, the section on "Natural History" attempts to bring together what is known of the history of the Hippoboscidae in nature, as distinguished from the structure and functions of their organs. Due to the scarcity of reliable observations on wild flies, it is based to a large extent on information obtained from the relatively few parasitic flies of domestic animals and on the results of laboratory experiments. It should be emphasized that conclusions drawn from this type of observation do not necessarily apply to flies living under natural conditions on wild hosts.

"Natural history" includes, besides the topics usually covered by the "ecology" or "bionomics" of some writers, certain types of instinctive behavior which perhaps are not always nor fully explained as direct responses to the environment. Regardless of whether or not the foregoing three terms are strictly synonymous, I shall use them interchangeably, much as I prefer the more old-fashioned word.

While the interrelations of organisms among themselves and with the environment show a bewildering variety, they are all expressions of the three fundamental organic needs for food, protection and reproduction, the first two regulating mainly the survival of the individual and the last that of the species. All three needs are always closely integrated and this is particularly true for insects with total viviparity, such as the Hippoboscidae, whose problems of feeding and protection are mostly solved at the same time for the adult and the offspring. All three aspects of hippoboscid life are dominated by the host-parasite relation, the final goal of their activities, which is correlated with nearly every detail of their

morphology and physiology. It will be both rational and convenient to group first the various aspects of their natural history under the three customary headings of nourishment, shelter and reproduction, and to conclude with a discussion of their host-parasite relation.

I. Food

The Blood Diet. It should be made clear at the start that the Hippoboscidae feed exclusively on fresh, fluid blood of warm-blooded vertebrates (homoiotherms). Under natural conditions, they are not known to drink water or to imbibe surface moisture either on or away from the host. Ormerod's (1900) statement that *Hippobosca equina* feeds on the perspiration given off by cattle in the summer, could not have been based on actual observation, since the mouth-parts of *Hippobosca* are scarcely built to absorb moisture from the surface of the skin. Adult louse-flies remain almost permanently on the food supply and do therefore not live under the same conditions as the tsetse-flies, although their feeding habits are essentially the same.⁸ When they stray from a live or dead host, either by accident or intentionally, they soon succumb for lack of food and shelter, unless they can reach a suitable new host. Both sexes of the Hippoboscidae suck blood.

Prouty and Coatney (1934) attempted feeding various substances artificially to *Pseudolynchia canariensis* (= *P. maura*), similar experiments having been successful with several other blood-sucking arthropods. Pigeon-flies confined in a glass cylinder were allowed access to a feeding tube closed with a membrane and filled with a variety of substances. No fly ever tried to suck cold food. Only the following materials were actually imbibed: fresh pigeon blood, kept at 94° F., on which one fly fed for 7 minutes, the abdomen becoming engorged and red; raisin juice; whole milk; bovine serum; and saturated sucrose solution. None of the flies fed artificially survived for a second meal. They died within from 2 to 117

⁸ It is generally agreed that vertebrate blood is the only normal food of the tsetse-flies and that it is essential for their reproduction. The claim that some species of *Glossina* may at times add to this in nature either water or vegetable juices, is based on very few observations, which, moreover, are far from convincing. It is true, nevertheless, that some tsetse-flies may be made to imbibe water from an artificial feeding apparatus, so that it is not unthinkable that such free-living flies might under unusual circumstances be driven by hunger to attempt abnormal feeding.

hours, their longevity being about the same as when kept completely starved under similar conditions of temperature and moisture.

The restricted nature of the food, at all stages of development, places the Hippoboscidae in a select group of strictly blood-sucking Arthropoda, which includes also the other pupiparous Diptera (Glossinidae, Streblidae and Nycteribiidae), certain small groups of Heteroptera (Polyctenidae, Cimicidae and Triatominae), the sucking lice (Anoplura), the ticks (Ixodoidea), and a few of the parasitic mites. No doubt it is significant that integral intra-uterine viviparity (or so-called pupiparity) occurs only among arthropods with a strict blood diet and is, moreover, confined to insects that feed mainly or exclusively on warm-blooded vertebrates. An exclusive diet of warm blood must have favored in some way the evolution of pupiparity to its present perfection, even though it did not perhaps induce it at the start.

Vertebrate blood is a concentrated type of food, hence one of the most desirable nutritive substances available. In addition to the highly nutritious essential components (plasma, red and white corpuscles), it is loaded with other organic and mineral ingredients, hemoglobin, vitamins and more subtle biotic substances, continually renewed and carried to all parts of the body. It is kept fluid and under pressure in walled vessels, some of which form a dense maze close to the outer skin, where it is readily accessible and easily ingested by means of properly constructed mouth-parts. The prevalence of hematophagy among several unrelated groups is sufficient proof that the Arthropoda have succeeded repeatedly, not only in discovering and reaching this choice source of food, but also in solving the more delicate physiological problems of assimilating it for their own metabolism.

A strict diet of fresh vertebrate blood calls for a suitable structure of the mouth-parts, as well as for special anatomical and physiological arrangements insuring the free inflow of blood and its proper digestion and assimilation. The description previously given of the proboscis leaves little doubt that the louse-flies are well equipped for blood-sucking. How this came about by evolution is not difficult to understand if we assume, as seems reasonable from the available evidence, that the Hippoboscidae are modified Muscoidea. Their ancestors acquired from the muscoid stock mouth-parts adapted to a liquid diet, calling only for further specialization. As a result, hematophagous habits originated several times independently among the Muscoidea, probably as soon as vertebrate

blood became available. The original incentive to puncture the skin, in order to tap this new and rich supply of food, may have been the more primitive dipterous habit of sponging either perspiration or other normal secretions of the skin, as well as blood and plasma oozing from wounds. Moreover, the labella of many non-biting Muscoidea bear asperities (*prestomal teeth*), sometimes sharp enough to scratch the skin and thus give the fly its first taste of blood. It should be pointed out that the very efficient, needle-like haustellum of the Hippoboscidae is duplicated almost exactly in the Glossinidae. These two families differ mainly in that the haustellum is not retractile within the rostrum membrane in the tsetse-flies, as it is in the louse-flies. This raises the possibility that both groups are rather closely related and that the ancestral Hippoboscidae may have acquired the present perfected mouth-parts, as well as the exclusive blood diet, before they became permanent ectoparasites.

The more intricate adjustments of digestion, assimilation and general metabolism needed by the change from a vegetable or mixed to a strictly sanguine diet, are not so easily explained. Perhaps they were gradually forced upon the flies during a transitional stage, when the ancestral forms fed at the same time on blood and on plant juices, as some other blood-sucking Diptera do to this day. The physiological peculiarities allowing a strictly blood-sucking insect to thrive on a diet of blood alone, are as yet scarcely understood, so that the following discussion is mainly an exposition of unsolved problems. Only two of the several mechanisms involved seem to have been investigated, though not in the Hippoboscidae.

When a blood-sucking insect feeds, it mixes with the blood its own saliva containing one or more enzymes, one of which is an anti-coagulin which prevents clotting. This process seems to be a refinement of an ancestral habit, retained by many other Diptera, of ejecting saliva on solid food in order to change it into a liquid suitable for ingestion. The precise constituents and action of the saliva of the Hippoboscidae are not known; but they may be analogous to those of the tsetse-flies, studied by Lloyd (1921) and Lester and Lloyd (1928). When the salivary glands were removed from living *Glossina tachinoides*, the flies survived for some time (usually from 7 to 14 days, in one case up to 58 days), meanwhile feeding on man and digesting normally, sometimes even producing healthy larvae. Glandless flies fed on fowl did not thrive so well. Eventually, however, such flies found it difficult or impossible to feed and particularly to digest, as the blood remained in the proboscis

and clotted in the crop, fore-gut and anterior portion of mid-gut, causing death by starvation. The experiments showed that injection of saliva in the host's tissues is not an essential preliminary to the act of feeding, but is rather incidental, since the salivary secretion and the blood mix at the very tip of the haustellum. The function of the saliva and of the anticoagulin it contains is to prevent the clotting of blood in the lumen of the haustellum, crop, fore-gut and anterior part of the mid-gut, so that the food remains fluid until it reaches the region of the mid-gut where digestion occurs. Saliva plays no part in digestion proper, as is shown also by its lacking digestive enzymes (Wigglesworth, 1929; 1950, p. 329).

In the tsetse-flies and presumably also in the Hippoboscidae, digestion and absorption are carried on in the posterior two-thirds only of the mid-gut, where the epithelium secretes a powerful coagulant and various digestive enzymes. A first question is whether the mid-gut enzymes alone are adequate for digesting blood or must be supplemented for this purpose from some other source. What digestive enzymes are produced by the louse-flies is again unknown. In *Glossina*, according to Wigglesworth (1929; 1950, p. 331), protease, which digests proteins (some of the main constituents of blood), is very active in the mid-gut, while carbohydrases are absent except a very feeble amylase in the same region. It should be stressed that digestion is rapid in the pupiparous Diptera. Even tsetse-flies, which imbibe $1\frac{1}{3}$ to $1\frac{2}{3}$ times their own weight of blood at one meal, usually feed again within 30 hours. A second problem is how an exclusive diet of blood may provide an insect with all the organic substances required for growth, reproduction and energy production, including the energy consumed in locomotion and in flight by the winged species. It is, of course, evident that the Hippoboscidae and other pupiparous Diptera thrive precisely on this type of diet; but exactly how do they achieve this? To what extent and by what method the various constituents of vertebrate blood are broken down for assimilation by insects have scarcely been investigated; although it is known that in certain blood-sucking insects hemoglobin disintegrates only partially, the remaining product being excreted directly.

It is now generally recognized that sterile vertebrate blood, the only food directly available to the Hippoboscidae and other pupiparous Diptera, is an inadequate or incomplete diet, since it is deficient in certain accessory substances, particularly certain vitamins, which are essential for growth and sometimes for normal reproduction (Wigglesworth, 1950, p. 348; 1952, p. 66). In some blood-

sucking insects these substances seem to be produced by micro-organisms living freely in the intestinal tract. It is difficult to conceive how the gut of the Hippoboscidae could become infected with outside bacteria or yeasts; such organisms might presumably contaminate the labella, when these come in contact with the surface of the skin, and then be taken up with the blood. Actually the lumen of the mid-gut of certain louse-flies harbors extracellular, presumably anaërobie and saprophytic micro-organisms. *Rickettsia melophagi* Nöller (1917), a unicellular, spheroidal or rod-like organism, which has been the subject of many investigations (see J. Bequaert, 1942a, pp. 195–196, for references), occurs in most sheep-keds, in Europe and North America, on the inner surface of the mid-gut, and is transmitted from the adult to the larva with the secretion of the milk-glands, surviving pupation. It does not seem to affect the health of the sheep-ked adversely, but on the other hand is not known to play a rôle in digestion. Aschner (1931, pp. 397–400) found a somewhat similar *Rickettsia*-like organism under the same conditions in *Lipoptena capreoli* (= *caprina*). He also described (1931, pp. 394–395) from the mid-gut of *Pseudolynchia canariensis* (= *Lynchia maura*) slender, thread-like bacteria, mostly free between the peritrophic membrane and the epithelium, but some also inside cells of the muscular coat surrounding the wall. His account of these organisms is rather confused and that of similar bacteroids in *Hippobosca camelina* (1931, pp. 395–397) is even less convincing, since he states that in this species they occur almost always inside epithelial cells. I suspect that these intestinal bacteroids of *Pseudolynchia* and *Hippobosca* might be only intracellular symbionts, such as will be discussed later, seen at a temporary extracellular stage. Steinhaus (1943; 1946, p. 44, fig. 15, and p. 245) described as *Corynebacterium lipoptenae* rod-like bacteria found chiefly in the lumen of the intestinal tract of all of 10 *Lipoptena depressa* taken from a deer near Hamilton, Montana.

Present evidence is altogether too slight to assume that the extracellular micro-organisms found normally in the mid-gut of certain louse-flies either assist in digestion or produce accessory food substances.

Intracellular Symbionts and Nutrition. In several types of insects every individual contains specific micro-organisms packed in specialized cells, so-called *mycetocytes*, usually of a characteristic shape. These cells are often grouped to form *mycetomes*, always located in or near the same organs in every species. Almost invariably some special mechanism assures the transmission of the or-

ganisms from one insect generation to the next. Because of these and other peculiarities, the intracellular organisms of the mycetocytes are now regarded as more than tolerated, innocuous parasites, but rather as messmates or *mutualistic symbionts* (symbiotes; endosymbionts), useful somehow to the insect. It is noteworthy that they occur generally in the strictly blood-sucking Pupipara and that the mycetomes of these flies are usually associated with the wall of the mid-gut. Since they have been found in all genera of the Hippoboscidae examined for the purpose, it is safe to assume that they occur throughout the family; indeed, Buchner (1952, p. 148) regards their presence as one of the characteristic adaptations of these flies, inherited from their early ancestors.

Mycetomes were first recognized by Sikora (1918) in *Melophagus ovinus*, where they have been frequently studied (Jungmann, 1918; Hertig and Wolbach, 1924; Anigstein, 1927; Zacharias, 1928; Glaser, 1930; Aschner, 1931; for more complete résumés, see Buchner, 1930, pp. 609-614; J. Bequaert, 1942a, pp. 196-197). The intracellular symbionts of the sheep-ked are of two types. All keds of both sexes examined in Europe and North America contain spheroidal or short rod-like organisms, which fill most of the protoplasm of enlarged epithelial cells. The infected cells form a large, ring-like mycetome at the bend of the right-side coil of the mid-gut (Fig. 15, *my*), along one-eighth to one-tenth of the length of the abdominal mid-gut. The symbionts are not "inherited" through the egg, but are transmitted with the secretion of the milk-glands to the larva, where they are stored until pupation in enlarged cells (mycetocytes) forming the epithelium of the anterior tubular portion (proventriculus) of the mid-gut. During pupation the larval mycetocytes are freed from the epithelium and maintain their individuality at first in the anterior part of the mid-gut. Zacharias (1928, pp. 695 and 703) states that about this time some of the mycetocytes break down, releasing symbionts which penetrate through the intestinal epithelium into the body cavity, where some were observed. He suggests that these symbionts might migrate then to the milk-glands, presumably passing through the secretory cells of the glands, although none were ever found there. In the mid-gut of the pupa the larval mycetocytes migrate backward and eventually break down, releasing the symbionts which now enter some of the epithelial cells of the newly-formed adult mid-gut.

Zacharias (1928, pp. 705-711) described from some only of the European sheep-keds a second, more slender, thread-like symbiont. This fills ordinary, flat, epithelial cells, usually of the mid-gut, more

rarely of the Malpighian tubules, and is said to be transmitted in the same way as the other type.

In *Lipoptena cervi*, symbionts were noticed first by Roubaud (1919, p. 532) and later by Zacharias (1928, pp. 711-717), in a mycetome located much as in *Melophagus*. They are also of two types and transmitted in the same manner. According to Aschner (1931, pp. 376-380), the symbionts of *Lipoptena capreoli* (= *L. caprina*) are in every respect like those of *L. cervi*. In *Lipoptena*, the mycetome extends over one-eighth to one-tenth of the length of the abdominal mid-gut.

The mycetome of *Ornithomyia biloba*, studied by Zacharias (1928, pp. 718-725; as *O. avicularia*⁹), differs markedly from that of the Melophaginae. The freshly dissected mid-gut of newly-emerged, unfed flies shows no distinct mycetome, but is swollen at about mid-length over a short stretch. When the gut is stained with borax carmine, the swelling discloses two lengthened, darker-stained areas separated by two narrow, paler bands. In cross-section, the epithelial cells of the dark areas are normal and contain no symbionts; but the layer beneath the epithelium is a mycetome, the several cells of which are fused into a syncytium with many nuclei and are filled with long, thread-like, twisted organisms, interwoven with the fibrillae of the muscle coat.

According to Mr. I. B. Tarshis (*in litt.*, 1951), the mycetome of *Stilbometopa impressa* is located as in *O. biloba* and has a somewhat similar structure. It shows, however, certain interesting peculiarities which he will describe in a future paper.

Aschner (1931, pp. 378-380) found that the mycetome of *Pseudolynchia canariensis* (= *Lynchia maura*) extends over a relatively short stretch of the mid-gut (about one-twentieth of the length of the abdominal part), where the epithelial cells are greatly enlarged. However, the symbionts in this case fill only the apical portion of the cells, nearest the gut cavity, and are disk-like or vesicular and difficult to stain. Similar organisms were found in the secretion inside the lumen of the milk-glands.

In *Hippobosca equina*, *H. longipennis* (= *H. capensis*), and *H. camelina* also, Aschner (1931, pp. 380-390) found symbionts in

⁹ Zacharias' flies were doubtless *Ornithomyia biloba* Dufour, since they were bred from puparia found in abandoned swallows' nests in Germany. Although often recorded by error as a parasite of the European barn swallow (*Hirundo rustica*), *O. avicularia* does not occur normally on this host or in its nests.

enlarged epithelial cells; the mycetome is very extensive, being continuous over six-tenths, five-sixths or six-sevenths of the length of the abdominal mid-gut. The organisms of *H. equina* are mostly rod-like and congregate in the basal portion of the cells, not apically as in *Pseudolynchia*. They are variously shaped in *H. longipennis* and *H. camelina*. In *Hippobosca* also the lumen of the milk-glands is infected with micro-organisms. The symbionts of *H. equina* were first seen by Roubaud (1919, p. 532), who regarded them as intracellular yeasts, and later also by Zacharias (1928, p. 717).

Aschner (1931, pp. 412-416) attempted to grow the intracellular symbionts of *Melophagus*, *Lipoptena*, and *Hippobosca* outside the insects, but without success. The extracellular *Rickettsia*-like organisms of the gut of *Melophagus ovinus* have been cultivated on various media by several investigators; Kligler and Aschner (1931) have grown successfully, not only those of *M. ovinus*, but the similar organisms in the gut of *Lipoptena capreoli* (= *L. caprina*), *Hippobosca longipennis* (= *H. capensis*), and *H. equina* as well.

The following peculiarities of the intracellular symbionts suggest a possible connection with digestive or other metabolic processes of the flies: (1) the regular occurrence in all strictly blood-sucking species, including besides the Hippoboscidae all the other pupiparous blood-sucking Diptera, and their absence in blood-sucking flies with a different larval diet; (2) the elaborate mechanism ensuring their transmission to the offspring of the fly; (3) the location of the mycetomes in the epithelium or the muscle coat of the mid-gut. Although such a combination of peculiarities in the same insect is unusual, it should be noted that, taken individually, some of these features occur also in other types of arthropods and for other types of micro-organisms. They may therefore be incidental and without any particular significance to the insect. Possibly the symbionts merely take advantage of the unique digestive set-up of the pupiparous flies, without giving much if anything in return. Intracellular symbionts are fairly widespread among the Arthropoda, even among the non-hematophagous types. Probably they originated from some of the extracellular, saprophytic or mildly parasitic micro-organisms, found frequently in the mid-gut of arthropods. Eventually some of the organisms invaded the epithelium of the wall of the gut, causing the tumor-like enlargement of certain cells or the formation of a syncytium, features which may have become hereditary in certain cases. The location and extent of the mycetomes vary with each species, possibly indicating that in certain areas of the gut the epithelial cells were originally more vulnerable, more ac-

cessible to invasion, or more suitable to the growth of the micro-organisms. As for the mechanism of transmission, this is actually no more intricate than that of many other parasitic micro-organisms of vertebrates transmitted by arthropods. Moreover, it is often nearly impossible to draw the line, either on morphological or on biological grounds, between the so-called "symbionts" and other innocuous or pathogenic micro-organisms occurring sometimes in the same species of arthropod.

On the other hand, there is ample proof that certain free-living, saprophytic or parasitic micro-organisms, morphologically similar to the symbionts of the Arthropoda, produce powerful biotic substances, such as hormones, vitamins and enzymes, or are able to fix directly free atmospheric nitrogen into organic products and to break down nitrogenous organic substances at least to the ammonia stage. This makes it most probable that the endosymbionts of the blood-sucking insects influence somehow the metabolism of their hosts. The possible physiological rôle of the symbionts, particularly those of arthropods with a specialized food diet, is now much in the limelight. Comprehensive accounts have been published by Buchner (1930), Aschner (1931, pp. 416-439), Steinhaus (1946, pp. 188-255; 1949, pp. 123-165), and Wigglesworth (1950, pp. 345-349). Latterly the whole subject was discussed from many angles by several specialists at a colloquium on the occasion of the IXth International Congress of Entomology (August, 1951) at Amsterdam (1952, *Tijdschr. v. Entom.*, **95**, pts. 1-2, pp. 23-196). The reader must be referred to these sources for the details, which seem irrelevant in the present work, since none of the observations and experiments refer directly to the symbionts of the Hippoboscidae.

Discussing the possible function of the symbionts in strictly blood-sucking insects, Wigglesworth (1952) concludes, from observations in the tsetse-fly (*Glossina*) and blood-sucking Reduviidae (*Triatoma*; *Rhodnius*), that the organisms are most probably not concerned directly in the digestion of the blood. There is evidence, however, in the sucking lice (*Pediculus*) and Reduviidae (*Triatoma*; *Eutriatoma*; *Rhodnius*), that they influence growth, metamorphosis and reproduction. It seems likely that they supply certain growth factors, presumably vitamins, in which sterile blood is deficient.

Differential Feeding and Host Specificity. Blood is an extremely complex substance. It also shows physical and chemical peculiarities among the several vertebrates, aside from the more obvious differences in the size, number and structure of the corpus-

cles. The proportion and composition of the mineral and organic components of the plasma are decidedly specific and fairly constant for each species. For instance, in the case of the blood proteins, particularly important elements in the diet of blood-sucking insects, not only does their concentration vary with the species, but they show also a more subtle serological specificity brought out by their antisera-antigen reactions. The differential properties of the blood of the several available hosts no doubt influence to some extent the ectoparasite's metabolism. In the Pupipara, which feed on blood only, such differences may have an important survival value, certain types of blood being better suited for continued, normal reproduction and others perhaps wholly unsuitable. Conceivably the effect of the type of blood diet upon the rate of reproduction has been the primary factor inducing by natural selection whatever host specificity is now observed in the Hippoboscidae. Other factors, such as the opportunities for shelter and the peculiarities of the ecology and behavior of the vertebrates, certainly contributed also toward determining the true breeding hosts of the flies; but I am inclined to regard them as of secondary importance.

It is unfortunate that so little attention has been paid to the possible rôle of differential feeding in the normal life of blood-sucking arthropods. A few, rather unsatisfactory experiments are available for the tsetse-flies. Lloyd (1914), in Northern Rhodesia, fed in captivity series of freshly caught, wild female *Glossina morsitans* separately on goats, monkeys, fowls, ducks and chameleons, recording the length of life of each fly, and the number of puparia and aborted larvae deposited, each puparium also being measured. Flies fed on chameleons did not produce larvae, perhaps because they failed to obtain a satisfactory blood meal. It was concluded that mammalian blood has a slight advantage over that of birds, as it seemed to be more easily digested. Puparia obtained on mammalian blood averaged larger than those produced by flies feeding on birds.¹⁰

I can find no experimental data bearing on the influence of various types of blood upon the reproductive rate of the Hippoboscidae. Coatney (1931) fed the pigeon-fly, *Pseudolynchia can-*

¹⁰ The results of Lloyd's experiments with *G. morsitans* have been criticized adversely on the basis of observations (not experiments) with *G. palpalis*. However, if the effects of differential feeding are specific, as may be suspected, they should not necessarily be the same for all species of *Glossina*.

ariensis, for about 2 weeks on domestic fowl in the laboratory, obtaining normal puparia meanwhile; but he does not compare his results with flies fed under similar conditions on the normal host. Kemper's (1951, p. 239) experiments with *Crataerina pallida* fed on abnormal hosts, particularly the domestic pigeon, furnish no information on the present topic.

Mechanism of Feeding. Two hundred years ago Réaumur (1742, p. 602), in France, described as follows how *Hippobosca equina* bites and sucks blood: "If I had been uncertain how these flies fed, if I had doubted that the very thin thread sometimes appearing in front of the head was actually a proboscis, as I have called it, my doubts would have been removed by an experiment performed without my trying. In spite of my efforts several spider-flies escaped from a pounce box where I kept them and from which I intended to remove one only. One of those that escaped did not go very far; after a fairly short flight it alighted on my arm. I was careful not to chase it away; I wanted to know whether it might not like to pierce my skin the same as that of a horse or an ox: it did not pause long to teach me that my blood was to its taste; it protruded the thin thread which I have called the proboscis and almost at once thrust the tip in my skin. The bite was felt no more than that of a flea. Horses must bear the bites of these flies with composure, if they are not more painful to them than this one was to me. The fly sucked my blood without stopping for nearly a quarter of an hour and during all this time I felt only a strong itching. The wound left open after the fly departed was marked only by a small red spot, which disappeared in less than half an hour and which produced no raised area: from which it follows that these flies are not as dreadful as mosquitoes, which do not fail to envenom the wounds they make. The fly was so engrossed with imbibing my blood, that it let me take my hand to a spot lighted by the sun's rays, where I could observe it at leisure under a lens with a 6 to 7 lines focus. At first the fly pushed in more and more of the proboscis; but once this had penetrated as far as wanted and apparently as far as possible, it was pulled out a little and then pushed back again as far as before. This process was repeated several times, but at unequal intervals. I saw then that the proboscis started from a sort of membranous pouch, oblong in shape and thicker close to the head than elsewhere. As long as the fly kept the proboscis inserted in my flesh, the two pallets [palpi] that enclose it in a sheath were spread apart in a rather broad angle, allowing the portion of the proboscis kept between them to enter the flesh. The fly

left only after being fully engorged, when its gaster was distended and tight with the blood that filled it." It may be interesting to compare the French naturalist's account with the following, more recent observations made on the same species in Spain by Hase (1927, pp. 218-233). When the proboscis is not in use, most of the haustellum is retracted within the rostrum membrane, only the apical portion with the labella being hidden within the slightly hollow sheath of the palpi. A fly about to feed takes a firm hold of the skin by anchoring the deeply divided, strong claws to the hairs or sometimes to the minute folds of the epidermis. Next it explores the surface, at first with the setiferous tips of the palpi, later also with the labella as soon as the tip of the haustellum protrudes from the slightly spreading palpi. During the preliminary probings the labella are often covered with a clear liquid, presumably saliva oozing from the hypopharynx. Differences in the temperature or toughness of the skin may possibly guide these explorations. A further eversion of the rostrum membrane frees the entire haustellum from the palpi, which do not guide its course nor take an active part in feeding. The prestomal teeth of the labella do the actual cutting of the skin, after which the haustellum bores in rapidly under the pressure of head and thorax, meanwhile bending forward and sideways, as well as twisting. The whole or part of the needle-like portion of the haustellum enters the skin, until the labella reach a capillary of appropriate size in the stratum corneum. If a suitable capillary is not found at a first try, the fly removes the haustellum and bores at another spot. The protruding portion of the rostrum membrane shows active sucking motions during the actual imbibing of blood. Near the end of the meal, the fly voids excreta from a previous digestion and eventually also some of the freshly absorbed blood. Cleaning motions with the legs, starting over wings and eyes, indicate near-satiation, the fly preparing to leave the spot of the bite. As a rule the haustellum is then easily and swiftly removed; but sometimes it can only be pulled out with an effort. Once feeding is well under way, the fly is not easily disturbed and ignores most of the stimuli to which it responds quickly at other times. Hase's drawings of six successive stages of the biting process are reproduced in my Fig. 6H. The duration of a complete blood meal varies greatly: in Hase's experiments several flies engorged respectively within 3, $7\frac{1}{2}$, 10, 14, 20 and $24\frac{1}{2}$ minutes (15 minutes on the average); one female fed without interruption for 43 minutes.

Jobling (1926, p. 345) describes the feeding of *Melophagus*

ovinus on Man in the laboratory: "Before the ked starts feeding it must attach itself to the host. As the human skin is very poor in hair much time is required before the ked becomes fixed. The ked then protrudes the haustellum between the maxillary palps, applying the end of the labellum to different points of the skin, apparently in search of a suitable spot for piercing. When such a spot is selected the insect pushes its proboscis against the skin with such force that the middle part of the haustellum bends into a bow. Sometimes in piercing the ked twists the haustellum as one twists an awl. Immediately afterward there can be observed forward and backward movements in the labellum, the distal part of the proboscis rapidly penetrating into the skin. The haustellum penetrates into the skin as far as two-thirds its length. The appearance of a red spot under the vertex indicates the blood being sucked into the oesophagus. All the keds fed under observation were gorged in about 10 minutes after the appearance of the red spot in the region of the oesophagus. It has also been observed that forcible removal of the feeding ked involves the risk of tearing off the haustellum, as it is fixed by the everted prestomal teeth to the bottom of the hole formed in the skin. I felt no irritation during the feeding of the sheep-keds, but four or five days later small yellowish papules made their appearance. Each had a very minute opening through which serum exuded. The irritation caused by these papules is not very severe, but they heal very slowly, disappearing three or four weeks after the feeding of the insects."

Brumpt (1913, p. 638) states that *Lipoptena cervi* engorges on Man in 12 to 20 minutes. Hase (1939, p. 414), in Germany, also made hungry, volant *L. cervi* bite Man, using flies caught in the open in November and brought to the laboratory. They engorge within 15 to 25 minutes. Once a suitable spot is selected by feeling with the palpi and probing with the haustellum, the latter is inserted in the skin, either obliquely or at a right angle, by pushing the head downward or sometimes also by forward thrusts of the whole body. While feeding, the fly remains as if "frozen" on the spot and is not disturbed by either touch or pressure or by moving its legs. When placed on mice, *L. cervi* attaches behind the ears and to the neck, moving to the darker belly when engorged without attempting to leave the animal. The mice seem to be annoyed not so much by the bite as by the crawling of the flies. One mouse succeeded in catching and chewing two of the flies but did not actually eat them. The deer-ked likewise starts defecating while feeding and eventually the feces contain some undigested or partly digested blood.

It is rather unfortunate that the foregoing observations on mammal-infesting flies were made on abnormal hosts (Man and mice) and usually performed in the laboratory. There is no certainty that they conform in every detail with normal feeding under natural conditions on the regular hosts. In particular, differences in the texture and thickness of the skin, density and nature of the pelt, and the individual reaction to the bites may influence the method and speed of feeding.

There are as yet few comparable observations of bird-flies. Kemper (1951, p. 236) states that if *Crataerina pallida*, kept without food 3 or more days in the laboratory, are put on the plumage of a swift, *Apus apus*, they usually slip at once under the feathers and presumably start feeding immediately. They select to some extent the belly and the neck, and have not been observed biting the head. Within 7 to 15 minutes (about 10 on the average) the flies reappear, mostly engorged, run for a short while over the body and eventually hide in the plumage, as a rule beneath the wings. Kemper induced the swift fly to feed on a tree sparrow, *Passer montanus*, a great tit, *Parus major*, and domestic pigeons. He observed that the fly did not enter the plumage as quickly on these strange birds as on the swifts. The duration and size of the meal were the same as on the normal host and the longevity of the flies seemingly was not impaired. No information is given as to the production of puparia. Attempts to feed the swift fly on guinea pigs and white mice failed.

Nöller (1920, p. 166) was unable to make *Ornithomyia biloba* (cited as *O. fringillina*) bite a crossbill, *Loxia c. curvirostra*, using flies taken from barn swallows, *Hirundo rustica*, or bred from puparia found in swallows' nests. Even when starved for 3 to 7 days, the flies refused to bite. This would seem to point to a strong selectivity in the choice of a blood supply by this species.

Schuurmans Stekhoven and his co-workers, in Argentina, recently observed how *Pseudolynchia canariensis* feeds on the domestic pigeon (unpublished observations). Newly-emerged flies fast one or more days before attempting to bite, while older flies taken from birds sometimes feed within a few seconds after being placed in a vial on the skin. After probing the skin with the palpi, they protrude and push in the haustellum. Meanwhile the fly rises on its hind legs, tilts the body forward, and rests on the fore tarsi and the strongly bent fore femora and tibiae. The palpi are spread out on the skin. The fly engorges within 5 to 10 minutes, during which time it is difficult to disturb. If the meal is interrupted, the fly usually starts feeding again at another spot. Defecation by feeding

flies was not observed. Huff (1932) kept *P. canariensis* for 2 to 8 days on the American mourning dove, *Zenaidura macroura carolinensis*, the fly feeding meanwhile. Kartman (1949), in Hawaii, also fed pigeon-flies on the Chinese dove, *Streptopelia chinensis*, and the ring-necked dove, *S. decaocto*; some were kept alive from February 29 to March 29 on the Chinese dove and from May 12 to July 4 on the ring-necked dove.

Olfersia aenescens is a specific fly of certain Oceanic birds. Kartman (1949), in Hawaii, placed 20 flies taken from a red-footed booby, *Sula sula rubripes*, in a cage with a domestic pigeon on February 29. Most of the flies showed no interest in the pigeon and died within a few days. On March 10, however, one surviving *O. aenescens* was recovered from the pigeon and showed fresh blood in the mid-gut; two other flies, bred from puparia, remained alive on a pigeon from April 24 to May 4.

Size of Blood Meal. Until now it has been generally believed that the diverticulum or storage crop of the fore-gut is atrophied and non-functional in all Hippoboscidae, and that the amount of blood they absorb at one meal is therefore limited by the capacity of the fore-gut and of the anterior, widened portion (duodenum) of the mid-gut. While this may be true for the sheep-ke, *Melophagus ovinus*, and possibly for other mammal-infesting flies, recent, unpublished observations by Mr. I. B. Tarshis show that in some of the bird-flies, particularly in *Stilbometopa impressa*, a certain amount of blood enters the diverticulum toward the end of the meal. Even in this case, however, the quantity of blood stored in the crop is relatively small and the fore and mid-gut remain the chief food reservoirs. Nevertheless, the total amount of blood imbibed at one meal may be very large, but varies greatly even under the best feeding conditions.

In Hase's (1927) experiments with starved *Hippobosca equina* fed on Man, one female weighed 31 mg. before and 35 mg. after a full meal, having gained 4 mg. or about 1/8 of its original weight. These figures were 31 mg. before and 43 mg. after feeding for another female, which gained 12 mg. or 1/3 of its weight.

Freund and Stolz (1928) found that *Melophagus ovinus* imbibes from 8 to 14.2 mg. of blood at each meal. A newly emerged ked nearly doubled its original weight, of 15.1 mg., to 29.3 mg. after feeding 10 minutes. In Kemper's (1951) experiments with *M. ovinus* fed on Man, 10 females imbibed at one meal slightly more than 10 males, the females gaining 3 to 15 mg. (8.1 mg. on the average) and the males, 6 to 13 mg. (7.4 mg. on the average).

Kemper (1951, p. 237) determined the size of the blood meal of the swift fly, *Crataerina pallida*. In this fly the length of the combined head and thorax is about the same in both sexes, but the abdomen is much wider and also longer in the female than in the male, whether unfed or fed. The female averages 7.41 mm. (6.9 to 8.1) in length and 3.15 mm. (2.9 to 3.5) in width when starved, 9.15 mm. (8.0 to 9.9) in length and 6.89 mm. (5.5 to 8.4) in width when engorged. The corresponding measurements of the male are 7.19 mm. (6.3 to 7.7) in length and 3.12 (2.9 to 3.5) in width, unfed, and 8.03 mm. (7.4 to 9.1) in length and 4.69 mm. (4.3 to 5.3) in width, engorged. Flies kept starved for 5 days increased their weight with one blood meal from the original 22.7 mg. to 59.0 mg. in the female, and from 18.4 mg. to 31.4 mg. in the male, in an experiment using 10 flies of each sex. Occasionally even more blood may be taken up in one meal: a female which had engorged more fully than usual weighed 91 mg.; after fasting 5 days its weight was down to 37.5 mg.; on the 8th day it voided a premature larva of 16 mg.; when it died on the 10th day it weighed only 12 mg.; it therefore had taken up at least 60 mg. of blood at one feeding, nearly 5 times the original unfed weight.

The amount of blood ingested by the hippoboscids compares favorably with the blood meals of the tsetse-flies, although the latter are provided with a large and fully functional storage crop. Macfie (1912) concluded, from experiments with *Glossina palpalis*, that the male of this fly imbibed on the average 27 mg. of blood at one meal and the female slightly more, or nearly $1\frac{1}{3}$ times the unfed weight for the male and $1\frac{2}{3}$ times for the female.

Frequency of Meals. Since permanent ectoparasites have the food supply within easy reach at all times, there seems to be no reason why they should not feed at fairly regular intervals, regardless of day or night, the changing seasons or the periodical activities of the host. However, little is known as yet of the time required to digest a full meal. Due to the feeding needs of the developing larva, digestion is probably more rapid in the female hippoboscids than in the males.

The undigested material of the blood and the products of excretion are eventually evacuated as feces. In many cases defecation starts toward the end of a feeding. Fecal matter first appears at the anus as a droplet of soft or semi-liquid material which hardens in the air, presumably by drying. A new droplet pushes the first farther out and the successive droplets usually adhere in bead-like strands, which eventually break up in shorter strands or in individ-

ual pellets or feculae. When the feculae are dry, they have a characteristic shape. Hase (1927, pp. 226-228, fig. 15) describes them for *Hippobosca equina*, and in a later paper (1939, p. 415, fig. 2) for *Lipoptena cervi*; Kemper (1951, pp. 245-246, fig. 7) for *Crataerina pallida* and *Melophagus ovinus*. Kemper observed that the feces of *M. ovinus* are softer than those of *C. pallida* and consequently build up only very short strands (about 3 mm. long), or none at all. On the other hand, the fecal strands of *C. pallida* may reach 15 mm. in length before breaking up. The feculae of *Pseudolynchia canariensis* will be described in a forthcoming paper by Schuurmans Stekhoven and his co-workers, in Argentina.

Hase (1927, pp. 230 and 232) found that one of his *Hippobosca equina*, fed on Man, refused to feed the first, second and third days after repletion, but fed readily on the fourth; another fly fed eagerly the third day after a full meal. Hase (1939, p. 411) also kept winged *Lipoptena cervi*, captured in the open, alive from 6 to 8 days in a humid atmosphere at 27° C., when they would suck blood every day on Man or on mice. At room temperature the flies died within 3 days. At 5° C. they became stiff and digestion was arrested, to be resumed when the temperature was raised. Some flies were fed on Man 6 or even 8 times on successive days and seemed to stay healthy. Four flies that had engorged the same day on Man, fed once more on a mouse the next day and again on Man the third day. Kemper (1951, p. 237) observed that in *Crataerina pallida* four to five days elapse between consecutive feedings.

In this connection, Mr. I. B. Tarshis (*in litt.*, 1951) made the interesting discovery that in *Stilbometopa impressa* the feeding requirements are not the same for both sexes. In the male the gut is at all times generally distributed in the abdomen, so that feeding may be resumed as soon as digestion is completed. In the female, however, while a larva is developing in the uterus, the gut is pushed far forward toward the fly's waist, thus making room for the development of the very large offspring. Throughout the period of gestation no blood is taken in by the female. She feeds once after voiding a larva and this blood meal lasts her until her next feeding after the deposition of the next larva, and so on. Just after feeding the female's gut is well distributed throughout the abdomen, as it is at all times in the male.

The information at present available on the size and frequency of the meals is inadequate to calculate the total amount of blood required for the full development of one larva, from the hatching of the egg until parturition, as well as the amount imbibed during the

average life of a fly. Such data might be useful to determine more accurately the damage done by feeding alone to the well-being of the host by an average hippoboscid population.

Resistance to Starvation. The ability to survive without food for some time must often be important to ectoparasites and particularly to forms emerging away from the host, as is the case for nearly all Hippoboscidae (except *Melophagus* and perhaps a few others). It would seem that as a rule newly-emerged, unfed flies withstand starvation better than those that have previously fed on a suitable host.

Curtice (1890) and Swingle (1913), in North America, concluded that *Melophagus ovinus*, removed from sheep and exposed to normal atmospheric conditions, dies within 3 or 4 days. In carefully controlled experiments, in Australia, Sweet and Seddon (1917) found that keds live from 2 to 11 days away from the host. They appear to stand dryness and lack of food best when the temperature is moderately low and uniform. Moisture is needed if extremes of temperature are to be withstood. In shorn or shed wool, life is always short and seems to be little influenced by the fed or unfed condition. Hill (1918), in Australia, experimented with large numbers of adults, unfed and fed, as well as of different ages, and under a variety of conditions. He states that they may survive away from the host longer than had been generally believed. One ked, kept in a cellar, lived for 18 days; two for 14 days under similar conditions; a few others, in a more natural environment, for 11 to 13 days. These were, however, exceptional individuals, for his tables show that 75 to 80 per cent of the starved keds died within 1 to 6 days. Graham and Taylor (1941), also in Australia, obtained similar results: newly-emerged keds survived in unfed condition for 4 to 5 days at 16° to 30° C. At lower temperatures life was prolonged to 14 to 24 days; while higher temperatures reduced it to as little as one day. Kemper (1951, p. 247), in Germany, was unable to keep fully-engorged sheep-keds alive for more than 7 days in a thermostat at 20° to 27° C., the majority dying within 5 days; but he may have kept the keds under too dry conditions.

Cowan (1943, p. 186) experimented with *Lipoptena depressa* in British Columbia. Survival tests were conducted upon newly-emerged flies and also upon sexually mature individuals removed from the host. Seven newly-emerged flies kept in an incubator at room temperature over damp sand, survived for 72, 48, 52, 60, 62, and 52 hours, respectively, the average for this sample being 57 hours. Individuals taken from a deer started dying approximately

24 hours after removal, the last surviving 6 days. Of 201 flies removed from the head and neck of a buck shot October 8, 90 per cent were dead 48 hours later. Flies seem to survive somewhat longer when left upon the dead host, a single living specimen being observed after 11 days, and several taken alive after 6 days and 8 days under such conditions. According to Cowan, the short survival time of the winged individuals must be a potent factor in limiting the population in areas where deer are scarce. Hare (1945a, p. 56), in California, also working with *L. depressa*, determined that newly-emerged adults may survive away from a host much longer than Cowan thought, if kept under proper conditions. Volants reared from normal puparia collected on a captive deer survived from 4½ to 8 days without food. Those caught in the open lived only up to 3¼ days if kept under daylight conditions, but up to 6 days if kept in the dark. In his experiments, 50 per cent of the reared flies settled successfully on a host 4 days after emergence. He concluded that under natural conditions volants might remain active for from 1 to 4 days. Theodor (1928), in Palestine, could keep newly-emerged *Lipoptena capreoli* (= *L. caprina*) alive for at most 2 days without feeding. Beebe (cited by Bequaert, 1942a, p. 130), in British Guiana, kept *Lipoptena mazamae* alive for 3 days after removal from the host.

Hase (1927, p. 200), in Spain, kept normal, hungry *Hippobosca equina*, removed from the host, alive usually for 3, exceptionally for 4 days in a dry atmosphere, and for up to 6 days under moister conditions, at 22° to 25° C. He believes that this fly withstands starvation better when the air is very humid. In experiments with *Hippobosca variegata* (= *H. maculata*), in Indonesia, Schuurmans Stekhoven found that most flies, kept away from the host without feeding, died within 1 or 2 days, the males usually somewhat before the females; a few females survived up to 3 days.

In Prouty and Coatney's (1934) experiments, in Nebraska, newly-bred *Pseudolynchia canariensis* (= *P. maura*) survived unfed for approximately 109 hours if left undisturbed; if disturbed by shaking, they lived for only 75 to 92 hours. Ed. and Et. Sargent (1909), in North Africa, had previously determined that this fly survives only 2 or 3 days when kept starved. A forthcoming paper by Schuurmans Stekhoven and his co-workers, in Argentina, describes further experiments on the resistance to starvation of pigeon-flies, most of them surviving 4 or 5 days.

Falcoz (1922, p. 228) kept 4 *Ornithomyia biloba* (cited as *O.*

avicularia), taken from a swallow's nest in France, alive without food for 6 days.

Galli-Valerio (1930, p. 214; 1932, p. 132), in Switzerland, noted that *Crataerina pallida* could live without food for from 3 to 5 days after being removed from swifts, *Apus apus*. Kemper (1951, p. 247) was able to keep this fly alive much longer in starvation: of 30 specimens kept at from 21° to 24° C. indoors, 23 lived 5 days and one survived 9 days; one exceptional overfed female lived for 13 days.

Cannibalism. The only information available on this point is a rather vague statement by Eysell (1924, p. 387): "In 1904 I made the interesting observation that hungry louse-flies bore into the blood-filled gut of members of their own species and imbibe the contents. The wound healed normally and the insects survived for weeks after." On p. 235 there is another brief reference to this case, from which it appears that the observation was made on *Melophagus ovinus* and that flies that had been attacked were fed again on normal blood, which explains their survival for some time after.

II. SHELTER

Adequate protection against adverse factors in the environment is essential for the welfare of the individual and hence for the survival of the species. The problem of how to secure this is solved neatly by the Hippoboscidae and other obligate ectoparasites, which use the source of food also as a permanent abode, thus eliminating many of the vicissitudes of a free life. To be successful in this, however, the ancestors of the louse-flies needed far-reaching structural and physiological adjustments or adaptations, which eventually led to such extreme specialization that their fate is now tied up irrevocably with that of the hosts. It may be pertinent to consider the peculiar environmental conditions offered by the body cover of birds and mammals and the manner in which they affect the bionomics of the flies.

Physical Characteristics of Feathers and Hair. From various considerations to be presented in Part II of this paper, it is believed that the earliest hosts of the ancestral Hippoboscidae were most probably birds, so that the peculiarities of plumage should be considered first. Feathers are unique horny products of the epidermal cells of the avian skin, not duplicated elsewhere in the animal kingdom, and the most outstanding characteristic of the birds. Typically a feather is a thickened and usually stiff main stem or quill, bearing an inner and an outer web or vane of softer barbs, which

are divided into barbules and these in turn into barbicels. The several parts, as well as the whole, vary greatly in size and shape. The outer or surface feathers are the relatively strong and elastic contour feathers, some of which become very large on the wings and tail, being then used for flight. Elsewhere on the body the contour feathers overlie the inner or under down feathers, which are smaller, more fluffy and often more numerous. In most birds the feather coat or plumage is a thick and compact, though light and elastic mass of regularly imbricated contour feathers, slanting backward or downward, thus forming a smooth outward surface and a nearly waterproof cover for the under down. From our present viewpoint, the plumage encloses most of the body in a comparatively thick layer of light, aerated and fairly waterproof material. Its elastic resilience guards the body against mechanical injury, while the blanket of air held in the interstices of the feathers insulates the skin, protecting it against rain and dampness and reducing the loss of heat by convection and radiation, particularly during flight. A microclimate of unusual uniformity for temperature and humidity prevails in the rather loose layers of feathers, as compared with that of the outside environment. In this respect bird plumage is clearly one of the most favorable biotopes for insect life. It should be noted that, owing to the lack of sweat glands in the avian skin, the air enclosed within the plumage never becomes oversaturated with moisture by perspiration when the temperature increases unduly. Excess body heat is released mainly through many air-sacs distributed throughout the body and connected with the lungs (Wetmore, 1921, p. 23). In addition, the insulating blanket of air in the plumage can also be regulated; pulling the feathers closer removes some of the air and increases the loss of body heat, while puffing them out reduces the loss by admitting more air, a method of heat regulation affecting the ectoparasites directly.

The inner body temperature of birds is known to average higher than that of mammals and to vary more among the several species as well as individually. It fluctuates also following changes in the bird's activity and for other causes; there seems to be no marked seasonal variation. According to Wetmore (1921), resident birds of cold regions become more heavily feathered before winter sets in and more thinly feathered for summer, thus decreasing or increasing radiation of heat from the skin. The inner temperatures of birds were investigated and summarized by Wetmore (1921) and by Baldwin and Kendeigh (1932). A short paper by Becker and Stack (1944) gives valuable data taken from live birds of 37 com-

mon species from the central United States (30 passerines, 1 wild dove, 1 quail and 5 Picidae), some of which are among the most frequent hosts of two common American flies, *Ornithomyia fringillina* and *Ornithoica vicina*. The average inner body temperature of these birds varied from 108.1° F. to 110.2° F., the maxima from 108.3° F. to 115.8° F., and the minima from 104.3° F. to 109° F. In *Turdus migratorius*, which showed the greatest variation, the temperature ranged in 48 birds between 105.2° F. and 115.8° F., the average being 109.5° F.

Wetmore (1921, pp. 18-21) also found that there is a marked difference in the temperature of nestling or young birds between the so-called precocial and altricial species. In the precocial birds, the young are fairly well feathered, able to run about and feed themselves as soon as they are hatched; their body temperature approximates closely that of the adult of the same species. The altricial birds, however, hatch in a weak and usually naked condition and require to be fed and protected in the nest for some time by the parents. Their nestlings show a lower average temperature than the adults. This was found to be the case for certain Columbidae (*Zenaidura*), Tyrannidae (*Myiarchus*), Hirundinidae (*Petrochelidon*), Muscicapidae (*Geothlypis*, *Dumetella*, and *Sialia*), and Paridae (*Penthestes*). The young of these birds are evidently dependent upon brooding by a parent to maintain their bodily heat. For instance, in the catbird, *Dumetella carolinensis*, the body temperature of 6 nestlings averaged 101.7° F., while it was 108.6° F. for the male and 108.7° F. for the female. Since some of the common bird-flies often parasitize altricial birds and show a decided preference for nestlings, the lower temperature of the young may be of some importance to them.

The inner body temperature regulates that of the blood on which the flies feed; but the surface body temperature controls the biotope of the insects. The skin temperature, derived from that of the body, is generally lower. It is less known than that of the body. Kallir (1931) determined the skin temperature of some 10 European species, as well as the variations for several areas of the body. Baldwin and Kendeigh (1932) found that the skin temperature of the American house wren, *Troglodytes aëdon*, is 0.8° F. to 3.9° F. lower than that of the body and differs in both sexes as well as in several parts of the body; it is not affected by moderate changes in the temperature of the air, being on the whole less variable than the body heat. In 9 males, the inner body temperature averaged 108.5° F., while the skin temperature was 107.2° F. on the belly,

105.5° F. on the breast, 106.7° F. on the side, and 106.6° F. on the back. In 15 females, the body temperature also averaged 108.5° F. (as in the males); the averages of the skin temperatures were: 107.2° F. on the belly (as in the males), 107.2° F. on the breast (higher than in the males), 106.7° F. on the side (as in the males), and 105.6° F. on the back (lower than in the males). It seems rather doubtful that such slight variations could seriously affect the presence, distribution over the body, or seasonal occurrence of hippoboscids on a bird host.

Although pelt, the hair cover of mammals, differs greatly from plumage, it is equally effective as a protective device. In most mammals the skin is more or less clothed with hair, a modified form of epidermis exclusively found in this class of vertebrates. Hairs are of different length, thickness, rigidity or softness, density, direction and color. Three main types, connected by transitional forms, may be distinguished (Noback, 1951). Guard hairs ("Leithaare" or "Borstenhaare" of Toldt, 1935) are fairly straight, evenly thick throughout or gradually thinner at the tip, and are sometimes modified into bristles or spines. Pile hairs ("Grannenhaare" of Toldt) or awns are also straight, but relatively thin basally and thickened over the apical portion. These two types form the overhair or upper fur, the major and coarser part of the pelt of many mammals, particularly among the Ungulates. The third type, or fur hairs ("Wollhaare" or "Flaumhaare" of Toldt), are much softer and finer, often showing a tendency to curl. They form the underhair or under fur, beneath the cover of guard and pile hairs, and give the woolly feel of most fur animals. Variations in the relative proportions of the three types of hairs impart to each species of mammal its characteristic pelt. These differences may be of some importance to ectoparasites in selecting or avoiding available hosts.

The pelt guards the body and especially the skin against mechanical injury, owing to the thickness, durability and resilience of the upper fur. It also protects against excessive atmospheric humidity, particularly fog, rain and snow, as well as against loss of body heat in a cold or windy environment. Insulation is achieved mainly by a series of thin layers of motionless air within the pelt (Herrington, 1951). The woolly under fur is a particularly effective insulator and is therefore as a rule unusually developed in animals apt to be exposed to extremely low temperatures. On the other hand, hair also helps cool off the body when it is exposed to excessive heat, inasmuch as the animal can erect the upper fur.

This releases some of the enclosed air layers and increases the surface exposed to the evaporation of moisture secreted by the sweat glands, which are present in the skin of most mammals (except the Carnivora and Rodentia).

On the whole, the texture and microclimate of the mammalian pelt seem less advantageous to ectoparasitic insect life than those of the avian plumage. Regardless of how they were acquired in the course of evolution, nearly all the peculiar external features of the majority of Hippoboscidae now function as near-perfect adaptations to life within plumage rather than within pelt. The general dorso-ventral flattening and correlated modifications of the body, notably the greatly widened sternum, the laterally attached and usually long legs, the slender and often deeply split claws, the emarginate notum, the wedge-shaped head, and the small, concealed third antennal segment, all combine to allow the fly to glide without hindrance or harm beneath the contour feathers, to move in any direction amid the down, and to maintain a firm hold while feeding or when the bird is moving. On the other hand, within the pelt of most mammals these structural peculiarities lose certain of their advantages. It is noteworthy that some of these features may be lacking in the mammalian louse-flies, possibly because they were never acquired by their ancestors; others may have been merely retained from the ancestral types of bird-flies from which the louse-flies of mammals were derived, without being now of any particular advantage. Certain mammal-infesting flies are noticeably less flattened than those of birds and all of them are decidedly less streamlined. However, the legs of the mammalian flies are shorter and often thicker, with a pair of heavier claws (sometimes unequal in length) than those of the bird-flies, enabling them to cling more securely to the coarse hairs of the rather loose pelt. It should also be pointed out that most mammalian pelts compare unfavorably with the average avian plumage as a protective cover against adverse climatic factors and potential enemies. The less effective hair cover may account to some extent for the paucity of louse-flies on mammals (34 species of 8 genera on mammals, as compared with 90 to 100 species of 13 genera on birds) and for the fact that their flies occur on fewer types of hosts than those of birds.

Effect of Macroclimate. The foregoing considerations might convey the impression that the behavior and distribution of the bird-flies, at any rate, must be relatively little influenced by the usual climatic factors, or macroclimate, of the host's environment. There is nonetheless evidence that these insects are by no means

completely immune to them. Many bird-flies show very little host specificity and therefore tend to occur over wide areas, some species being nearly cosmopolitan (such as *Lynchia albipennis* and *Ornithoica confluenta* of wading birds) or circumpolar or Holarctic (such as *Ornithomyia fringillina* and *Olfersia fumipennis*). This feature may obscure the effect of climatic conditions. Yet it is noteworthy that *Ornithomyia fringillina* and *Lynchia americana*, two of the most common bird-flies of temperate North America on a variety of hosts, are practically unknown in the Neotropics. Since they must be carried occasionally to tropical America by some of their migratory hosts, failure to become permanently established there can only be due to some adverse macroclimatic factor. On the other hand, like most of the Hippoboscidae, the majority of the American bird-flies are essentially tropical and subtropical insects, only some of them spreading normally or accidentally to more temperate or colder areas, particularly along the eastern Atlantic seaboard. Such species as *Ornithoica vicina*, *Ornithoctona erythrocephala*, and *Ornithoctona fusciventris*, which reach southeastern Canada, are scarcely permanent members of the local fauna in the northernmost part of their range. They should be regarded there rather as seasonal migrants, the adults and possibly even the puparia being normally absent during the winter. In these northern areas, these flies are most probably introduced anew in the spring by the migratory hosts returning from the south, at least after severe winters.

A low average yearly temperature and extreme cold during the protracted winter are the two main factors limiting the northward extension of the Hippoboscidae. The normal limit for the family in the New World is at about the 50th parallel, north of which the bird-flies at any rate are scarcely part of the autochthonous fauna. Among many hundreds of American bird-flies examined in recent years, only half a dozen *Ornithomyia fringillina* were from Alaska at the following localities: Crater Mt., on a "Columbia falcon"; Nelchina River, north of Mt. Witherspoon, N. W. of Valdez; Takotna, 63° N., 156° W., on *Canachites c. canadensis*. Old Crow River, Timber Creek, Yukon, about 68° N., 140° W., at present the northernmost New World locality for an avian hippoboscid, is near the annual isotherm of 20° F. In the eastern part of the continent, where the flies stay much farther south, the northernmost record is for an *Ornithomyia fringillina* (recorded as *avicularia*) taken by Eidmann (1935, p. 99) from *Junco h. hyemalis* on the Matamek River, in the southern Labrador Peninsula (15° 17' N.); this local-

ity is also near the annual isotherm of 30° F. As some of the passerine birds known in North America as hosts of *O. fringillina* migrate in the summer to the Arctic Circle or even beyond the scarcity of hippoboscids in the Far North must be due to the climate being unsuitable even in summer. No louse-fly has ever been taken in Greenland.

The Hippoboscidae of birds extend farther north in Europe than in America, which agrees with the more northern course of the annual isotherm of 30° F. in Scandinavia, where it approaches or even exceeds the 72nd parallel. The Holarctic *Ornithomyia fringillina* is known from Iceland, Scotland, the Shetlands, northern Scandinavia and northern Finland. I have seen this fly from Levajak on the Tana River, Finland, between 69° 45' and 70° N., the northernmost locality known for any hippoboscid. The other species of northern Europe, *Ornithomyia avicularia*, *Stenopteryx hirundinis*, *Crataerina pallida*, and *Olfersia fumipennis*, do not occur north of the Shetlands, southern Scandinavia and southern Finland, where the climate is about that of southern Canada and the northeastern United States.

The effects of climatic variations in the relative humidity of the air are more subtle than those of the temperature and therefore more difficult to discover. They should not be discounted, however, since it has been shown that certain Hippoboscidae are averse to excessive moisture, as I pointed out in discussing various tropisms of the flies. Mr. H. Hoogstraal, who has had much experience with the several species of *Hippobosca* infesting domestic animals in Egypt, informed me recently that these parasites are relatively scarce in the Nile Valley proper and the Delta, but increase in numbers as one travels toward the drier or desertic areas.

Macroclimatic factors also might possibly account to some extent for the periodic fluctuations in successive years of the hippoboscid population in the same locality. Herman (1937, p. 164) noted that at North Eastham on Cape Cod, Massachusetts, *Ornithomyia fringillina* and *Ornithoica vicina* were much more numerous on trapped passerine birds during August, 1937, than during August, 1936. According to information he received from Mr. C. L. Whittle, the reverse was true for these two years at Peterboro, New Hampshire. In 1937 there was practically no rain during July on Cape Cod, while in New Hampshire there was more rain in July, 1937, than the previous year. Herman suggests that perhaps hippoboscid flies thrive better in a drier atmosphere; but it might be difficult in this case to dissociate the temperature factor

from the atmospheric humidity, since in the northeastern United States summers with a heavier rainfall are generally cooler than those of drier years. It is known that the temperature influences the rate of reproduction of the louse-flies, the puparia requiring more time to produce flies in cool weather.

Pseudolynchia canariensis is thus far the only bird-fly whose range has been affected appreciably by man. At first mainly a parasite of wild Columbidae and diurnal birds of prey in the Old World tropics, whence it occasionally strays to Central Europe, it has become a regular parasite of domestic pigeons, on which it was carried by man at one time or other no doubt to nearly every part of the Earth. Yet it is far from being as cosmopolitan as its domesticated host. It failed to become established in Europe north of the 45th parallel, while in America it is rarely seen north of the 40th parallel. The few sporadic captures in pigeon lofts or on feral pigeons in New York and Boston are exceptional and probably seasonal. There is no evidence that either the adult or the puparium could survive a normal winter in the northeastern United States (J. Bequaert, 1943b).

No doubt owing to the poorer protection provided by hair pelt, the louse-flies of wild mammals are more sensitive to the macroclimate than those of birds. Their range is always more restricted, although this may be due in part to the more sedentary habits of the hosts. Most species are strictly tropical and the few that venture into colder temperate areas seldom extend as far north as their potential breeding hosts (*Lipoptena cervi* in Europe and Asia to 60° N.; *L. depressa* in northwestern America to 50° N.; *L. mazamae*, a tropical species, only to about 34° N. in the eastern United States).

Seven species of hippoboscids, *Melophagus ovinus*, *Lipoptena capreoli*, *Hippobosca equina*, *H. longipennis*, *H. rufipes*, *H. camelina*, and *H. variegata*, now use domesticated mammals as normal breeding hosts. Although some of these flies have been spread unintentionally by Man over wide areas, none has been able to become established over the same territory as its host and none is actually cosmopolitan. The sheep-keď, *M. ovinus*, the most successful of them, nowadays has only the domestic sheep as a normal breeding host; but the common assumption, often repeated in textbooks, that sheep carry kedcs wherever they are kept, is erroneous, as shown by an analysis of the known distribution (J. Bequaert, 1942a, pp. 183-186). Kedcs are either entirely lacking or occur only as temporary introductions in many areas where sheep are regularly kept. They avoid particularly the hot tropical and sub-

tropical lowlands, as well as many oceanic islands. The climatic factor which eliminates the ked after its introduction in unsuitable territory appears to be the high air temperature. It has been observed that at higher ambient temperature sheep-keds move away from the skin to the outer wool (Swingle, 1913; Hoffmann, Roth and Lindquist, 1950; Evans, 1950, p. 467). *M. ovinus* is the hippoboscid which reaches farthest north, as it extends close to the Arctic Circle in Alaska, Iceland, the Faroës and Lapland. In the Southern Hemisphere it occurs on the Falkland Islands (52° S.). *Lipoptena capreoli*, a specific parasite of the domestic goat, is at present restricted to the eastern Mediterranean countries and north-western India, where subarid conditions prevail. It shows no tendency to spread outside this area with its host. *Hippobosca equina*, the cattle and horse louse-fly, not known at present from a wild host, is a common parasite of equines and cattle in many tropical and subtropical parts of the Old World, extending northward to a few disconnected areas as far as southern England and southern Sweden. It is, however, by no means uniformly distributed over this territory, since it occurs only as exceptional and temporary introductions in Africa south of the Tropic of Cancer (J. Bequaert, 1931, pp. 310-311). Even more remarkable is its failure to become established in the New World, although it must have been introduced there repeatedly with horses. *Hippobosca longipennis* (= *H. capensis*), the dog-fly, is fairly common on a variety of wild Carnivora in East Africa; it is chiefly an abundant parasite of domestic dogs in many Mediterranean countries and southern Asia, extending northward as far as northern China. In Africa it avoids the moister tropical areas, being unknown from most of West Africa and the Congo Basin. It is also not found in Indonesia, Australia and the New World. It could scarcely have failed to reach America from time to time, yet has never become established there. *Hippobosca variegata* (= *H. maculata*), another horse and cattle fly, without known true wild host, is very abundant over the northern half of Africa, India and Indonesia; but again, it has never been able to gain a foothold in the New World. The climatic or possibly other factors which restrict the spread of these abundant parasites of cosmopolitan domestic hosts should be investigated more carefully.

Preferential Distribution on the Host. Many ectoparasites tend to select certain areas of the host's body in preference to others. This is particularly true of the biting and sucking lice, where two or more species living on the same individual host may each be restricted to its own area of the plumage or pelt, thus avoiding com-

petition. Little such topical selectivity is exhibited by the Hippoboscidae, presumably due to their great mobility, the generally light individual infestations and the scarcity of infestations with more than one species of fly. On birds, the flies are, moreover, difficult to locate, being usually concealed on undisturbed hosts, while they either leave or scatter over the body if the bird is handled or otherwise disturbed.

There should be, however, a certain amount of topical preference, conditioned by such factors as the feeding facilities, differences in the temperature and moisture of the skin, and variations in the possibility of escaping the destructive preening and cleaning efforts of the host. As pointed out before in discussing the sense organs, some louse-flies are sensitive even to relatively slight changes, particularly in the temperature. Unfortunately, little information is now available on the surface temperature of mammals and birds in different parts of the body. That such topical differences may be substantial is shown by Kallir's (1931) study of the European turtle dove, *Streptopelia turtur*, in which variations up to 3° C. were observed. The lowest temperatures (38° to 39° C.) were in the plumage of head and croup; the highest on the sides of the rump and near the anus (over 41° C.) as well as on the back and beneath the wings (nearly 41° C.). The topical variations of the skin temperature of *Troglodytes aëdon* were mentioned in the general discussion of the body temperature of birds.

The uneven distribution of *Melophagus ovinus* over the sheep's body has often been noted. It was most carefully studied by MacLeod (1948), in England. He found that, in winter and early spring, the upper side wool is equally if not more favored by the keds than the lower side wool, and that an appreciable concentration occurs on the back. With the advancing warm season, the keds tend to forsake the upper surfaces. The lower wool, including the abdomen, a site little favored in winter, now becomes the principal territory. The chest and throat are favored throughout the year, but particularly in winter and spring. Evans (1950, pp. 470-472), also in England, offers further statistical evidence in support of these conclusions and emphasizes the periodic migrations of the keds on the sheep's body.

Cowan (1943, pp. 183 and 185) studied the distribution of *Lipoptena depressa* over the body of coast deer, *Odocoileus columbianus*, in British Columbia. He states that there is a strong tendency for the gravid keds and their clasping mates to congregate on the lower surface of the host from the base of the

neck to the abdomen. On hot summer days, large numbers of flies frequently move about over the outer pelt. One deer in mid-August showed many crawling over the face and legs in nature.

Hippobosca equina and *H. variegata*, of cattle and equines, often cluster in numbers under the tail and between the thighs. Gachet (1915) reports that the dog-fly, *Hippobosca longipennis* (= *H. canina*), in Iran, frequently was observed biting sleeping dogs on the nostrils and at the edges of sores. Speiser (1907, p. 5) stated that East African specimens of *H. struthionis* were said by the collector to occur mostly beneath the ostriches' wings; it may be that the unusually heavy plumage made the detection of the flies difficult elsewhere.

There are as yet few observations on this topic for the bird-flies. They suggest that the flies seek out areas of the body where there is a better chance of escaping the destructive pecking endeavors of the host. For instance, *Olfersia fossulata*, the common parasite of the guanay, *Phalacrocorax bougainvillei*, on the coast of Peru, often selects the bird's head and neck, as shown on a photograph by Dr. R. C. Murphy (1924, *National Geographic Magazine*, 46, p. 294). The photograph by Dr. J. P. Chapin (Fig. 21) of *Olfersia aenescens* infesting the red-tailed tropic bird, *Phaëton rubricauda*, on Ducie Island, shows a similar preference of the flies for the neck and upper breast. It is also interesting to note that several specimens of *Ornithoica vicina*, which had strayed onto young domestic fowl in Virginia, were all on the head. Büttiker (1944), in Switzerland, observed that *Crataerina pallida* stays mainly on the neck and head of the swift, *Apus apus*.

Protective Behavior. Even the fully-winged species of Hippoboscidae rely mainly on running and hiding in order to escape danger while on the host. The wings seem to be used more to reach a host after emergence, in some cases at mating time, and when the flies are forced to leave a dead host and seek a new one. While winged louse-flies are not among the swiftest or most skillful fliers, they are nevertheless not as slow and clumsy on the wing as might be supposed. They take off and alight rather quickly, but their flights are always jerky and short. *Hippobosca equina*, for instance, which has rather powerful wings, flies when disturbed a distance of $\frac{1}{2}$ to 1 meter or less and then alights suddenly. Hase (1927, p. 193) observed also that it rises sometimes from the host for a brief, sharp turn in the air, to alight again close to the spot it had left on the skin.

Roberts (1925) observed an unusual behavior of *Hippobosca*

equina in North Wales, England, where it is very common and well established in the open in certain areas. In the summer the fly is abundant on both horses and cattle on bright, sunny days, but much rarer on cold and rainy days. Its distribution is closely correlated with the dense covering of bracken fern (*Pteridium aquilinum*) on certain hill slopes. During the day flies are seen occasionally sunning on the fern fronds; at sunset or when a spell of cold weather or rain is imminent, they generally leave the host and seek shelter on the under side of the fronds where they spend the night.

Whether fully-winged or subapterous, most Hippoboscidae run swiftly and skilfully through the pelt or plumage of the host. The long legs inserted at the extreme sides of the flattened thorax, and the unusually developed mid and hind trochanters allow them to move without having to raise the body, with equal ease and rapidity in every conceivable direction, forward and backward as well as sideways, as Dufour (1845) first pointed out for *Hippobosca* and *Ornithomyia*. The running motions of *Hippobosca equina* were studied by Hase (1927, pp. 194–196), who states that it may cover 3 to 7 cm. per second, its movements amid the hairs being greatly helped by the flattened body and particularly by the wedge-shaped head. Many of the bird-flies run even faster than *Hippobosca*, especially the subapterous species, which must rely on running alone for their safety and for reaching a host. The swift-fly, *Crataerina pallida*, studied by Kemper (1951, pp. 249–251), is extremely agile; it does not travel far in one stretch, usually a distance of 5 to 10 cm., sometimes only 2 to 5 cm., exceptionally 31 cm. In unfed condition, it covers about 5 cm. per second (calculated from 6 flies) and slightly over 4 cm. per second when fully engorged (calculated from 4 flies). Eichler (1939, p. 215) claimed that *C. pallida* could in addition perform small jumps; but Kemper was unable to confirm this and thinks that the jerky motions of the fly may have simulated jumps. Büttiker (1944, p. 28) observed on one occasion that *C. pallida* used the reduced wings to glide a short distance in the air. Schuurmans Stekhoven and his co-workers, at Tucumán, Argentina, determined the speed of *Pseudolynchia canariensis* by allowing flies to run in a glass tube 75 cm. long and 11 mm. wide (unpublished observations). As a rule this fly does not run very far before stopping for a few seconds: one fly covered the 75 cm. in four stretches or "heats," at speeds of 108, 300, 330 and 166 cm. per minute for each successive heat. The highest speed observed was 540 cm. per minute. This fly often moves the wings also while on the run.

The Melophaginae, or ked-flies of certain mammals, are exceptional in the family for their rather slow movements. Hase (1939, p. 412), in Germany, noted that winged, unfed *Lipoptena cervi*, of European deer, are rather slow runners, usually covering 0.5 to 1 cm. per second, rarely 2 cm., on an open surface, away from a host and unhampered by hairs. The apterous *Melophagus ovinus* manages to move about a great deal on the host, in spite of the short and thick legs; but its gait is very slow and clumsy. According to Freund and Stolz (1928), it covers from 6 to 12 cm. per minute, with an average of 8.5 cm., as compared with the 240 to 300 cm. per minute of *Crataerina pallida*. Kemper (1951, p. 251) noted that a crawling *M. ovinus* makes rapid grasping motions in the air with the fore legs before putting them down, no doubt in attempts to grab a host.

In *Allobosca crassipes* of the lemurs, in Madagascar, the legs are even shorter and much more swollen than in *Melophagus*. Mr. H. Hoogstraal, who observed this insect alive on the hosts, informs me that it is slow moving and secretive, keeping in the pelt near the roots of the hairs.

Most Hippoboscidae exhibit a strong positive thigmotropism (or stereotropism) and flatten the depressed thorax and abdomen against the host's body or any other surface. Even a decapitated *Hippobosca equina*, placed on its back, turns over at once so that the sternum and venter touch the support, after which it remains motionless on the spot, the fly being evidently warned of its normal or abnormal position by the many tactile setae (Hase, 1927, p. 202). H. A. Macpherson (quoted by Austen, 1926, p. 254) noted that, if a *Crataerina pallida* is surprised in a swift's nest away from a bird, it often flattens the body against the background and remains motionless. Cowan (1943, p. 185), in British Columbia, found that the tropistic responses of *Lipoptena depressa* change with age. Newly-emerged, volant or recently deälated, unfed flies of both sexes show a strong negative geotropism, always moving upward, either in a tube or on any object within reach. They are also positively phototropic, moving toward the light, but this tropism is secondary to the negative geotropism. Winged individuals seem to prefer light to dark clothing when alighting on a person. On the other hand, deälated flies that have fed for some time tend particularly to cling to any small object or to each other when removed from the host, a positive thigmotropism not noticed in the newly-emerged individuals. If several *L. depressa* of different ages are placed in a vial, the older individuals cling together in a mass at the bottom of

the vial, while the younger keds climb actively, each by itself. Prouty and Coatney (1934, p. 252) found *Pseudolynchia canariensis* (= *P. maura*) positively thigmotropic, seeking to push its way into small cracks or under the edge of pads or sheets of paper; this may explain why the female prefers to larviposit in rather tight cracks. According to Kemper (1951, p. 252), *Crataerina pallida* also turns over immediately to a normal position when placed on its back. *Melophagus ovinus*, however, is unable to turn over to the right position, unless its legs can grasp a near-by object (Freund and Stolz, 1928; Kemper, 1951). The peculiar tropistic responses of the louse-flies no doubt help them in escaping their enemies. They certainly make their capture unusually difficult.

Predacious Enemies. It is generally recognized that the hosts themselves are by far the most dangerous enemies of all ectoparasites. This important fact should not be overlooked when studying the effects of external factors or changes in diet upon populations of such arthropods. Any circumstance that either enhances or impairs the host's vitality and efficiency in combating its ectoparasites, tends to decrease or increase the parasitic population. Irritated by the bites or by the movements of the parasites, the host attempts to destroy them by every possible means, such as preening, rubbing, scratching or catching in mouth or bill, or even devouring them. It is not unthinkable that certain peculiar activities of birds, such as bathing in water or dust, smoke-flights and "anting," are more or less deliberate attempts to get rid of annoying parasites (Rothschild and Clay, 1952, pp. 125-128). It is improbable, however, that such methods are very effective against the swift Hippoboscidae.

Ed. and Et. Sergent (1906), Drake and Jones (1930), and Coatney (1930) noted that domestic pigeons fight *Pseudolynchia canariensis* by pecking and thrusting the bill in the plumage, thus destroying many flies. Austen (1921, p. 122) observed: "It was found in Palestine that an infested pigeon on returning from a flight, instead of at once seeking its resting place, as these birds usually do, would alight on the floor of the loft and proceed to stamp and peck itself."

Grimshaw (1911, 2, p. 86), while examining the contents of the crops and gizzards of red grouse, *Lagopus scoticus*, in England, found grouse-flies, *Ornithomyia fringillina* (= *O. lagopodis*), in 3 young birds, 28 to 40 days old: one fly in the gizzard of one bird and 2 flies in that of another; and one fly in the crop of the third bird.

Herman (1944, p. 114), working with *Stilbometopa impressa* of California quail, *Lophortyx californica vallicola*, observed that several flies placed in a cage with one or 2 quail yielded many puparia, while an equal number placed with 7 quail produced very few or no offspring. The birds were seen eating flies that leave the host temporarily when it becomes excited, as flies exposed in the open have little chance of escaping capture when many birds are confined in a small space. When 25 flies were placed in an escape-proof cage with 7 quail, 24 hours later only one fly could be found after extensive examination; but 17 flies were recovered 3 days after 18 flies had been placed in a cage with 2 quail only. Mr. I. B. Tarshis also noted that California quail eat their flies and found in addition that the birds catch the smaller *Lynchia hirsuta* more easily than the larger *Stilbometopa impressa* (unpublished observations).

Some years ago, Dr. C. M. Herman made the following interesting unpublished observation on a chipping sparrow, *Spizella pusilla passerina*, on Cape Cod, Massachusetts: "This bird, originally with 3 specimens of *Ornithoica vicina* and heavily infected with *Haemoproteus*, was placed in a gauze-covered cage about one foot on each side. During a period of one week 117 specimens of *O. vicina*, taken from various hosts, were placed in the cage with this sparrow. At the end of this period the bird was removed and examined. Only 2 flies were found. Further flies were then planted in the cage with the bird and kept under close observation. The flies would periodically leave the bird to rest on the gauze wall and then return to the host. Every so often, en route, they would become a cherished part of the bird's diet."

Sheep eat *Melophagus ovinus* regularly and in large numbers, this being the only known way in which they become infected with a blood protozoan, *Trypanosoma melophagium*, part of whose life cycle necessarily occurs in the ked (Hoare, 1923; Turner and Murnane, 1930). Newman and Cordeaux (1871), in England, noted that sheep "pluck themselves of keds." Evans (1950, p. 467), also in England, saw on several occasions "sheep biting keds from the surface of the fleece and then devouring them. This procedure was very marked during warm weather when some of them were on the surface of the fleece, and after shearing when the sheep were able to pick off keds without much difficulty. During colder weather, when the insects were in the depth of the fleece, the sheep had to be content with biting the fleece in an attempt to rid itself of the irritation."

Theodor (1928, p. 316), in Palestine, observed goats removing goat-keds, *Lipoptena capreoli* (= *L. caprina*), from the hairs with the lips and eating them. As in the case of *Trypanosoma melophagium*, the goat thus becomes infected with a similar protozoan, *Trypanosoma theodori*, which goes through part of its life cycle in the *Lipoptena*.

Modeer (1785), Girard, (1885), Neumann (1888), Evans (1950, p. 467), and others report that various birds, such as crows, starlings, wagtails and magpies, will catch and eat keds on sheep. Unfortunately there is no confirmation of this habit by actually finding keds or their puparia in the stomach of any of the birds. Dixon (1944) mentions that the California jay, *Aphelocoma californica*, was seen picking "ticks and deer tick flies" from the back of mule deer in Sequoia National Park, California. This statement again needs confirmation by examination of stomach contents.

Melin (1923, p. 21) saw an asilid fly, *Dioctria hyalipennis* (Fabricius), which had captured and was sucking an *Ornithomyia* sp. in Sweden.

Freund and Stolz (1928, p. 105) mention incidentally that, in Timor, Indonesia, they were told of a large hornet, *Vespa auraria nigrithorax*, eating the louse-flies of horses. Schuurmans Stekhoven himself did not observe any insect predator of *Hippobosca* in Indonesia; he was informed (1926, p. 47) that another person on the island of Soemba witnessed a fossorial wasp capturing *Hippobosca variegata*. These two statements should be confirmed by more careful observations, since they may be due to some confusion. The wasps may have been catching horse-flies (Tabanidae), which are the usual prey of certain species of fossorial wasps and more easily caught than *Hippobosca*.

According to Dr. W. W. Wirth (*in litt.*, 1946), on Rabbit Island, off the coast of Oahu, Hawaiian Islands, spiders were seen catching *Olfersia aenescens* resting on rocks in the rookeries of noddly terns and shearwaters.

Parasites. Compared with the free-living arthropods, most permanent ectoparasites of vertebrates are unusually free of parasites of their own, presumably owing to the more effective protection afforded by the host's body cover. In the Hippoboscidae, in addition, the more vulnerable puparia are few, widely scattered, and usually hidden either in the pelt or plumage or away from the host. It is doubtful that any of the parasitic organisms discussed below reduce appreciably the total population of a louse-fly species. In view of the very low rate of reproduction, few losses are needed

to maintain the population in a state of equilibrium and these are mostly caused by accidental injuries and by the predacious activity of the hosts.

1. **Bacteria and Bacteria-Like Organisms.** Under this heading will be grouped a variety of micro-organisms, including true bacteria, so-called bacteroids, true *Rickettsiae*, and *Rickettsia*-like organisms. They are conveniently studied together, particularly since it is often difficult to draw the line among them. Moreover, certain authorities regard even the *Rickettsiae* as merely a peculiar type of bacteria (Family Rickettsiaceae). At first sight, it might seem important or at least useful to distinguish between extracellular and intracellular organisms. This again does not always prove feasible in practice. No doubt some of the micro-organisms observed in insects never enter tissue cells, while others live normally inside cells; but some seem to have both an intra- and an extracellular stage. I am satisfied that the forms mentioned in the sequel are true organisms and not waste or other metabolic, inert products of the tissues. Several of them grow and multiply on appropriate media or in tissue cultures outside the insect's body, and in cases where cultivation has failed thus far, the organisms are similar to those that can be maintained in culture.

A previous discussion of the blood diet of the Hippoboscidae considered at some length many of the micro-organisms reported from these insects, so that only a summary, with more complete bibliographic references, need be given here. I commented at that time upon the scarcity of such organisms and particularly of the extracellular types in these flies.

Corynebacterium lipoptenae Steinhaus (1943; 1946, p. 44, fig. 15, and p. 245), described as a true bacterium of the Family Mycobacteriaceae, was found in Montana in the deer-ked, *Lipoptena depressa*, chiefly in the intestinal tract. It was successfully cultivated first on egg fluids and later also on other media. *C. lipoptenae* should be compared with various micro-organisms reported from *Lipoptena cervi* and *L. capreoli* in the Old World; perhaps also with *Corynebacterium ovis*, known from domestic sheep and reported also from mule deer in British Columbia (Humphreys and Gibbons, 1942).

Bacillus anthracis Cohn, the bacterium causing anthrax, is stated by Zumpt (1939, p. 704) to have been found in the gut of sheep-keds, *Melophagus ovinus*, taken on sheep which had died from anthrax. He also cites presumably unpublished experiments

by Bongert, in which anthrax is claimed to have been transmitted from infected to healthy sheep by the bite of keds. It is particularly in South Africa, where *Hippobosca* is sometimes unusually abundant on domestic animals, that investigators have been interested in the rôle such flies might play in anthrax epidemics. This possibility was investigated carefully by Viljoen, Curson and Fourie (1928). They state that *Hippobosca rufipes* is very common in South Africa, often appearing in the thousands on horses and mules, while cattle run on the same farm are relatively free from it. They note that anthrax is generally confined to equines, even where susceptible cattle and sheep freely mingle with them. The anthrax swellings were observed to start on the places where the flies cluster and to extend from there to adjoining parts. *Bacillus anthracis* was actually isolated from *H. rufipes* taken on horses infected with the disease. The epizootic form of anthrax occurs only during the summer, when louse-flies are particularly numerous on horses. It would seem therefore that *H. rufipes* is an important factor in the mechanical transmission of the disease in South Africa. Of course, there are several other ways in which anthrax is spread from diseased to healthy animals.

True *Rickettsiae* and similar organisms are common in the sheep-ked, *Melophagus ovinus*, in the lumen as well as in the epithelial cells of the mid-gut, and also in the milk-glands of the female. They were briefly mentioned in the discussion of the blood diet of the flies. *Rickettsia melophagi* Nöller (1917b, p. 70) was described and named from extracellular forms abundant nearly everywhere in all keds of both sexes, forming a layer over the cuticula of the epithelium in the lumen of most of the mid-gut. Notwithstanding unsubstantiated claims by Nöller and Kuchling (1923), Gordon (1933), and Katić (1940), it seems fairly certain that the organism is not inoculated to sheep by the ked and that it is not pathogenic either to the insect or to vertebrates. Although the transmission from ked to ked is not completely elucidated, it is most probably acquired by the larva feeding on the infected secretion of the female's milk-glands.¹¹ It has been cultivated outside keds on certain media. The intracellular *Rickettsia*-like micro-

¹¹ Jungmann (1918) claimed that he found the "ova" of *M. ovinus* infected with *R. melophagi*. His "ova" were not the true eggs (in the ovaries), but larvae developing in the fly's uterus, a confusion commonly made by non-entomologists unaware of the peculiar reproduction of the Hippoboscidae.

organisms of *M. ovinus* have not been given a specific name and it is as yet a moot question whether or not they are more than developmental forms of *R. melophagi*. They are usually regarded as mutualistic symbionts and are of two types. One form, apparently of general occurrence, fills the protoplasm of enlarged, specialized cells of a ring-like mycetome in the posterior portion of the mid-gut. A second form, different in shape, was found by Zacharias (1928) in some keds only, filling ordinary, flat epithelial cells usually of the mid-gut, rarely of the hind-gut or of the Malpighian tubules. Both types are harmless to the insect and are not transmitted to the sheep. According to Zacharias, some of these organisms occur freely in the lumen of the milk-glands of the female, whence they pass with the secretion of the glands to the alimentary tract of the intra-uterine larva. Here they enter specialized epithelial cells in the anterior portion of the mid-gut, close to the oesophagus. Zacharias describes also the complicated mechanism by means of which the symbionts reach the final mycetome of the adult during nymphosis. The micro-organisms of the sheep-ked are favorite study objects, so that the literature dealing with them is voluminous, as shown by the following references: Nöller (1917b), Jungmann (1918), Sikora (1918), Hindle (1921), Arkwright and Bacot (1922), Arkwright (1923), Nöller and Kuchling (1923), Kuchling (1924), Hertig and Wolbach (1924), van Thiel (1925; 1926), Anigstein (1927), Zacharias (1928), Glaser (1930), Buchner (1930), Aschner (1931), Kligler and Aschner (1931), Katić (1940), and Steinhaus (1946, pp. 244-245 and 312-315; see also pp. 205-206 for Kligler and Aschner's method of cultivating the micro-organisms).

The extracellular and possibly symbiotic intracellular bacteroids of *Lipoptena*, *Hippobosca*, *Ornithomyia*, *Stilbometopa*, and *Pseudolynchia* were discussed before in the section dealing with their possible rôle in digestion. It was stated that intracellular symbionts, located in mycetomes of the wall of the mid-gut, probably occur in all Hippoboscidae. Whether this is true of the extracellular forms also is more doubtful; and there is a possibility that the extra- and the intracellular forms in the same fly may be stages of one and the same organism. Both the bacteria-like and the *Rickettsia*-like forms vary in size and shape: *R. melophagi* may be spheroidal or coccoid, 0.4 to 0.6 μ in diameter on the average; or more elongate and rod-like, 0.5 to 0.6 μ in length and 0.3 to 0.4 μ in width. The intracellular symbionts are often very long and thin, thread-like, even simulating spirochetes. *Spirochaeta melophagi*

Porter (1910), described from the gut, ovaries and puparia of *Melophagus ovinus*, in England, was perhaps based on bacteroids escaped from ruptured mycetocytes. No spirochetes have been reported since by the several investigators who studied the micro-organisms of the sheep-ked.

2. Protozoa. The relatively few types of Protozoa known at present from the Hippoboscidae belong to the two classes Mastigophora (or flagellates) and Sporozoa.

Flagellates of the Family Trypanosomidae are very common in insects, some species being restricted to invertebrates, while others have both a vertebrate and an invertebrate host. In the latter case, the organism has at least a stage in the blood of the vertebrate, being often called a hemoflagellate; while the invertebrate host is invariably blood-sucking and acquires the flagellate by feeding on the infected vertebrate. At least part of the life cycle of the flagellate occurs in the invertebrate's intestinal tract. In most cases the vertebrate must acquire the flagellate from the invertebrate host, which usually, but not always, inoculates the protozoan with the mouth-parts while feeding. Both the vertebrate and the invertebrate are therefore essential links in the perpetuation of the hemoflagellate.

In the Hippoboscidae, hemoflagellates are known at present only from the keds, or mammalian flies of the subfamily Melophaginae. The best-known is *Trypanosoma melophagium* (Flu) (= *Crithidia melophagia* Flu, 1908), originally regarded as a specific flagellate of the ked, where it was first seen and described by E. Pfeiffer (1905) in the lumen of the mid-gut, in Germany. It is now recognized that the forms in the ked are developmental stages of a trypanosome found in the blood of most domestic sheep, for which it is not pathogenic. Laboratory-bred, clean keds have been infected experimentally by feeding them on the blood of sheep harboring trypanosomes. The flagellate upon reaching the alimentary tract undergoes a definite cycle of development: a so-called crithidial stage is produced in the mid-gut, followed by forms ineffective for sheep (metacyclic trypanosomes), which line the walls of the hind-gut. According to experiments by Hoare (1921; 1922; 1923*a*; 1923*b*) and Turner and Murnane (1930), infected keds do not inoculate the trypanosome by the bite (proboscis), but by the contaminative method, by way of the sheep's mouth. Sheep become infected by biting keds off the fleece and crushing them in the mouth, the metacyclic trypanosomes presumably penetrating through the buccal mucous membrane. In all experiments in

which emulsions of infected keds were fed by mouth to clean sheep, the latter acquired the trypanosome; while control experiments to infect clean sheep either through the abraded skin or by the bite of infected keds, invariably failed. In addition to the authors cited above, *T. melophagium* was also studied by Swingle (1909; 1911a; 1911b), Georgewitch (1910), Annie Porter (1910), C. F. Bishop (1911), Cauchemez (1912), Chatton and Delanoë (1912), Dunkerly (1913), Laveran and Franchini (1914a; 1914b; 1919a; 1919b), Nöller (1917; 1919), Kleine (1919), Böning (1920), Witzky (1922), Sprehn (1922), Buchner (1922), E. R. Becker (1923), Boese (1923), Nöller and Kuchling (1923), Kuchling (1924), Bozhenko and Tzeiss (1928), Colas-Belcour (1931), and Wotton (1940). A well-illustrated account of the life cycle of this parasite is given by Wenyon (1926, 1, pp. 502-507). Bishop (1911) claimed that he saw crithidial forms of *T. melophagium* in a tick of sheep, *Ixodes ricinus*, in England; this finding has not been confirmed. Bouvier *et al.* (1951, p. 276) mention briefly that H. Gaschen found *Melophagus rupicaprinus* of the chamois, *Rupicapra rupicapra*, in Switzerland, infected with "*Herpetomonas melophagae*"; these may have been developmental stages of a trypanosome of the chamois.

A hemoflagellate, first seen by Adler (1926) in the digestive tract of the goat-ked, *Lipoptena capreoli* (= *L. caprina*), in Palestine, and also studied by Theodor (1928), was later called *Trypanosoma theodori* by Hoare (1931). Theodor recognized that it is a stage in the invertebrate host of a non-pathogenic trypanosome found in the blood of domestic goats. The developmental cycle is similar to that of *T. melophagium*. Newly-emerged *L. capreoli* are never infected. If kept on an infected goat, the ked acquires the trypanosome in from 5 to 22 days. The scarcity of the trypanosomes in the blood of infected goats explains the slowness and the low rate of infection of the keds. In a herd of 15 goats, presumably all infected, on 2 animals all keds were negative, on 11, from 6 to 70 per cent of the keds were infected, and only on 2 were all keds infected. In the ked, the flagellate occurs in the mid- and hind-gut, never in the fore-gut, proboscis, salivary glands or other organs. Theodor established that reinfection of the goat is not by active inoculation through the bite or by the feces of the ked, but by infected keds being crushed by the goat. Even emulsions of infected keds injected subcutaneously failed to inoculate the trypanosome.

Herman (1945, p. 21) reported an unidentified flagellate from

the intestinal tract of *Stilbometopa impressa* from the valley quail, *Lophortyx californica vallicola*, in California; and Mr. I. B. Tarsis (*in litt.*, 1952) observed a similar organism in the same fly. The affinities of this flagellate have not been elucidated. It is not impossible that the organism may be a developmental stage of the trypanosome which Herman (*loc. cit.*) observed in the blood of the valley quail. In the course of his experiments with pigeon malaria, Aragão (1927), in Brazil, found domestic pigeons sometimes infected with *Trypanosoma hanna*e Pittaluga (1905, *Rev. R. Acad. Cienc. Ex. Fis. Nat. Madrid*, **2**, No. 3, p. 356). He observed that 12 *Pseudolynchia canariensis* (= *Lynchia maura*), bred from puparia and fed on a pigeon infected with the trypanosome, showed 4 days later some crithidial flagellates in the gut and more of them on the 8th day. Two squabs bitten by presumably infected flies and 2 others inoculated with saline emulsions of 3 flies containing many flagellates, all failed to show trypanosomes in their blood for the next two months.

In the Class Sporozoa, only the Order Haemosporidia is definitely known to occur in the Hippoboscidae. The complete development of the Sporozoa usually comprises both an asexual and a sexual cycle. In the Haemosporidia, the two cycles alternate: the asexual cycle (schizogony) occurs in a vertebrate, eventually producing gametocytes in the blood, and most of the sexual cycle (sporogony) in an invertebrate, starting with the formation of a zygote in the digestive tract and ending in a form infective to the vertebrate. The blood parasites (hematozoa) of this order are usually classified in two families.

The family Plasmodiidae consists of one genus, *Plasmodium*, which comprises the true malarial parasites of Man and other vertebrates. Although such parasites are frequent in birds, there is no evidence that the sporogony of any of them is completed in the Hippoboscidae or any of the other pupiparous Diptera, or that these flies transmit them to new vertebrate hosts.

The Haemoprotozoa, with the two genera *Haemoproteus* and *Leucocytozoon*, are of much interest to the student of the Hippoboscidae. At the asexual or schizogony stage, they are frequent parasites in the blood system of many birds and some reptiles, at first in the endothelial cells of the blood vessels and later (as mature gametocytes) inside the circulating cells or blood-corpuscles. The sexual or sporogony stage proceeds in a variety of invertebrate vectors. So far as known, no hippoboscid is involved in this sexual phase of any species of *Leucocytozoon*. There is, however, con-

clusive evidence for two species of *Haemoproteus* of birds that the further development of the gametocytes into mating gametes and the resulting sporogony occur normally in the digestive tract of certain Hippoboscidae. Eventually an infective form, or sporozoite, is produced in the fly and may be inoculated by the bite of the insect into a new avian host. In these species the bird-fly is therefore an essential link in the transmission from infected to clean birds, hence in the perpetuation of the hematozoa. The fly is also a second true host of these organisms, which are as much parasites of it as of the bird.

Of the two cases, *Haemoproteus columbae* Kruse (1890, p. 370) is the one for which the evidence for a normal transmission, from bird to bird by a louse-fly in nature, is most satisfactory. This blood parasite occurs frequently in domestic pigeons, *Columba livia*, particularly in tropical and warm temperate regions, and is the causative agent of a serious malaria-like disease. There is fully reliable experimental proof that it is normally transmitted from pigeon to pigeon by the bite of the pigeon-fly, *Pseudolynchia canariensis*, after undergoing sporogony in the insect. The names *Lynchia maura*, *L. lividicolor* and *L. capensis*, sometimes cited also among the vectors of pigeon malaria, are all synonyms of *P. canariensis*. As for *Lynchia brunea*, mentioned by Aragão (1907; 1908) as one of the vectors, it was based on a misidentification of *P. canariensis*, the true *Pseudolynchia brunnea* (Latreille) having nothing to do with the transmission of the disease; moreover, Aragão synonymized his *L. brunea* with *L. maura* in a later paper (1927, p. 827). At one time Aragão (1916, p. 353) included *Microlynchia pusilla* (Speiser) among the bird-flies transmitting *H. columbae* in Brazil; unfortunately he never described his experiments with this fly. *Microlynchia pusilla* is a strictly American bird-fly, known from a variety of hosts, among them 4 wild American species of Columbidae; it has also been taken a few times as a straggler on domestic pigeons in the New World. Its possible rôle in the transmission of *H. columbae* and other closely related hematozoa of native American doves, such as *Haemoproteus sacharowi* and *H. maccallumi*, deserves to be investigated more carefully.

Haemoproteus lophortyx O'Roke (1929a) causes a grave malaria-like disease in California quail, *Lophortyx californica*. The parasite goes through the sporogony stage of its life-cycle in the digestive tract of two species of flies, *Lynchia hirsuta* and *Stilbometopa impressa*, both commonly found on quail in western North America, and which act as the vectors of the disease.

Although the sexual stages of *H. columbae* and *H. lophortyx* should be regarded as true parasites of the bird-flies in which they develop, it is not known to what extent these hematozoa affect adversely the health or life expectancy of the insects. In the bird hosts they are decidedly pathogenic. For this reason their transmission by the flies will be considered more in detail in a later section of this work, while discussing the effect of the hippoboscids on their hosts, an important aspect of their host-parasite relation. Meanwhile it may be noted that the three Hippoboscidae definitely known at present as vectors of malaria-like diseases are among the most host-specific of the bird-flies. In domestication, *Pseudolynchia canariensis* is a regular parasite of pigeons, having been carried by man on this host to many parts of the world. In the Old World, its original home, it has a wider host range, as shown in the sequel. Both *Lynchia hirsuta* and *Stilbometopa impressa* are restricted to the New World, where their only breeding hosts are quail and related game birds of the family Phasianidae.

In the Class Cnidosporidia, the Order Microsporidia contains many parasites of insects, usually more or less pathogenic to them. None have been reported to date as occurring normally in the Hippoboscidae. However, Fantham and Porter (1913) claim to have produced the experimental infection of *Melophagus ovinus*, by way of the mouth-parts, with *Nosema apis* Zander, the causative agent of a disease of the honeybee.

3. **Fungi.** The supposed fungi which certain observers have reported from the internal organs of the Hippoboscidae were bacteria or related micro-organisms, discussed in earlier sections. Of the several groups of true fungi that normally or occasionally parasitize arthropods, only the Order Laboulbeniales, of the Class Ascomycetes, is thus far known to occur on some of the louse-flies. The Laboulbeniales are peculiarly shaped fungi, of small size, all strictly ectoparasitic on the outer integument of a variety of Arthropoda.

These fungi are by no means rare on other pupiparous flies of the families Nycteribiidae and Streblidae; but thus far they were practically unknown from the Hippoboscidae. Previously they were only mentioned briefly by Speiser (1905a, p. 359) in the description of his *Pseudolfersia mycetifera*, based on a male from an "eagle" on Senafir Island in the Red Sea. Recently I examined the type of this fly, now at the Vienna Museum, through the courtesy of Dr. F. Keiser, and recognized that it belongs to *Olfersia fumipennis* (Sahlberg). The specific name *mycetifera* alluded to

the presence of two clusters of what the author correctly recognized as Laboulbeniales, as I was able to confirm. Speiser stated that these fungi were to be studied by Brunnthaler; but I could not ascertain that they were ever mentioned again in print.

Actually the Laboulbeniales are not so very rare on hippoboscids. They have been merely overlooked, owing to their very small size and to the fact that they shrivel beyond recognition on dry specimens or are destroyed in the process of mounting the flies on slides. My attention was first called to them on a specimen of *Allobosca crassipes* from Madagascar. Shortly afterward I recognized them on the type specimen of Walker's *Ornithomyia simplex*, at the British Museum, my identification being confirmed at the time by Mrs. F. L. Balfour-Browne. Some time later I was able to enlist the competent interest of Mr. Richard K. Benjamin, while he was a Graduate Student in the Department of Biology of Harvard University. Mr. Benjamin, who makes a special study of the Laboulbeniales, agreed to go over the several hundreds of louse-flies preserved in spirit, which I had accumulated over the years. The result has been most gratifying, as shown by the subjoined list of the specimens found infested thus far.

Subfamily Ornithoicinae

1. *Ornithoica pusilla* (Schiner).
 - a. Female on *Dacelo leachii intermedia*, from Dobodura, New Guinea.
 - b. Female on *Dacelo gaudichaud*, from Hollandia, Dutch New Guinea.
 - c. Female on *Tyto aurantia*, from New Britain.
 - d. Female on *Ninox odiosa*, from New Britain.
 - e. Female on *Accipiter virgatus gularis*, from Loquilocon, Samar, Philippine Islands.
2. *Ornithoica stipituri* (Schiner).
 - a. Male on *Coracina* sp., from Dobodura, New Guinea.

Subfamily Ornithomyiinae

3. *Ornitheza metallica* (Schiner).
 - a. Female on *Halcyon chloris* (subsp.), from Boang Island, Tanga Group, Bismarek Archipelago.
4. *Lynchia pollicipes* Ferris.
 - a and b: Female and male on *Megalaima a. asiatica*, from Myitkyina, Burma.
5. *Lynchia schoutedeni* J. Bequaert.

- a. Female on *Anhinga r. rufa*, from Katwe, Toro, Uganda.
- b. Female on *Anhinga r. rufa*, from Kampala, Uganda.
- 6. *Lynchia (Ornithophila) simplex* (Walker).
- a. Female (type), without host, from Menado, Celebes.
- 7. *Microlynchia pusilla* (Speiser).
- a. Male on domestic pigeon, from Cali, Valle del Cauca, Colombia.
- 8. *Olfersia bisulcata* Macquart.
- a. One of 6 flies taken on *Sarcoramphus papa*, at Cayari Island, Uassa Swamp, State of Pará, Brazil.
- 9. *Olfersia aenescens* C. G. Thomson.
- a. Female on *Sula sula rubripes*, from Kaneohe Bay, Oahu, Hawaiian Islands.
- 10. *Olfersia fumipennis* (Sahlberg).
- a. Male, type of *Pseudolfersia mycetifera* Speiser, on an "eagle," presumably the osprey, *Pandion haliaëtus*, from Senafir Island, on the coast of Arabia, in the Red Sea.

Subfamily Alloboscinae

- 11. *Allobosca crassipes* Speiser.
- a. Female on *Lepilemur* sp., from Ambavoloana, Madagascar.

The fungi have now been found on 11 species belonging to 6 genera in 3 of the 6 recognized subfamilies. It is doubtful, however, that they occur on the Hippoboscinae and Melophaginae, as very many specimens of these two subfamilies have been examined. Practically no Ortholfersiinae were available for this particular search.

The material will be fully studied and described by Mr. Benjamin in the near future; but he has kindly furnished the following information of more general interest, with permission to use it in my work. Probably 3 or 4 distinct species are represented in the present collection. It is of particular importance that they all belong to the one genus *Trenomyces*, of the family Peyritschiellaceae, and that this genus was previously known only from the biting louse (Mallophaga). All of the hippoboscoid fungi are minute, even for the group to which they belong, being among the smallest Laboulbeniales known. The largest species barely reaches 0.6 mm. in length when fully developed and most of them are considerably smaller. They are dioecious, as usual in *Trenomyces*. They show, however, the unusual peculiarity of being anchored to the integument by means of a long rhizoid (or root), which is sometimes as

long as the free fungus and penetrates beyond the cuticle in the epidermal cells of the fly. In most other Laboulbeniales the rhizoid is very short and limited to the cuticle of chitin and sclerotin. These parasites do not seem to prefer any particular location on the fly. For instance, of the two infested *Lynchia pollicipes*, one bore them on the left side at the base of the abdomen, the other on the base of the left wing. On the type of *Lynchia simplex*, they grew from the dorsal side of the metathorax, right behind the scutellum. The *Ornithoica pusilla* from Samar carried a thick growth of fungi along the hind margin of the abdomen.

It may also be noted that the *Trenomyces* are known thus far only on hippoboscids from the tropical parts of the Old as well as the New World. Although very many flies were examined from North America and Europe, none were found infested.

4. **Parasitic Mites (Acarina).** Certain Acarina are the most common ectoparasites of the Hippoboscidae, but are known thus far only from bird-flies (Ornithoicinae and Ornithomyiinae). They are of more than passing interest as they seem to be connected with specific parasitic mites of birds, although the details of the relation are at present obscure. The life-history has not been elucidated for any of the species and the published accounts are confused.

The oldest genus reported from bird-flies is *Microlichus* Trouessart and Neumann (1888, p. 134), originally proposed as a sub-genus of *Symbiotes* and based on *Chorioptes avus* Trouessart (1887, p. 923). The female of *Microlichus avus*, more fully described and figured in 1888, was found imbedded in the skin of a domestic sparrow, presumably in France, no exact locality being given. Trouessart and Neumann stated that they found absolutely similar female mites in the skin of three other species of birds from Europe, South Africa and the Antilles; that all these mites were conspecific seems difficult to believe. They also referred to *M. avus* a single male taken from a dead sparrow at Vegesack, near Bremen, Germany. Vitzthum (1934) doubted that this male was conspecific with the original female and thought that the true male, as well as the eggs and immature stages, of *M. avus* were as yet unknown. He referred to *M. avus* a female from Belgium, as it agreed with Trouessart and Neumann's figure of the species. This female was found by Collart on the body, not on the wings, of an *Ornithomyia avicularia* and was not surrounded by eggs. For this reason Vitzthum surmised that *M. avus* was not a parasite of *Ornithomyia*, but that it used the fly only to reach a new bird host, where the mite digs in the skin and starts a brood. According to M. Leclercq

(*in litt.*), the fly on which Collart found *M. avus* was the true *O. avicularia* and was collected at Glain, Belgium, on a blackbird, *Turdus merula*.

Another mite of the same genus, *Microlichus uncus* Vitzthum (1934), is somewhat better known. Females were found fixed to the wings of 9 *Ornithomyia biloba* near Liege, Belgium, no doubt from *Hirundo rustica*, the normal host of this fly. Vitzthum (1934) and Collart (1934) called the flies *Ornithomyia fringillina*; but M. Leclercq, who examined them at the Brussels Museum, recognized that they were *O. biloba* Dufour, as Eichler (1939b, p. 222) had surmised. The additional *Ornithomyia* from Brussels, August 8, 1918, on which Collart (1934, p. 2) said he found more *M. uncus*, was likewise *O. biloba*. All were listed as *O. biloba* by Bequaert and Leclercq (1947, p. 81).

In spite of published statements to the contrary (Ash, 1952, p. 30), the male, larva and nymphal stages of *M. uncus* have not been described and it is not definitely known where they occur. Collart (1934, p. 2) stated that he found on the flies, amidst the eggs of *M. uncus*, a few larvae, but these were not described nor mentioned by Vitzthum. Collart stressed that all 21 female mites were fixed on his 9 flies to the under side of both wings, invariably at one of the following three definite, clearer points of the veins: about midway on the upper margin of the second basal cell, at the extreme basal elbow of the same cell, and a short distance beyond the base on the lower margin of the anal cell. Most of the female mites were surrounded or hidden by compact clusters of from 1 to 25 eggs. Usually one, more rarely 2 or 3 such clusters occurred on each wing and on one or both wings. Collart believed that the mites select the wing veins deliberately, neglecting the body, and that they even prefer the clear basal elbow of the second basal cell; perhaps the clearer, less sclerotized stretches of the veins are more easily pierced with the hypostome in order to suck the blood circulating in the wing veins. In general, however, the mites infesting the Hippoboscidae do not show such precise selectivity on the body of the fly, as will be shown later for the American species. A female *O. biloba* from a cliff swallow, *Riparia rupestris*, at Banyuls-sur-Mer, France, recently sent by Mr. J. Théodoridès, carried a few mites with eggs on the under side of one wing, but many more on one side of the thorax behind. Mr. Théodoridès informs me (*in litt.*, 1951) that Mr. J. Cooreman named these mites *Microlichus uncus*.

In order to determine whether female mites prefer certain parts

of the flies, only attached mite clusters with eggs should be noted. Upon reaching the fly from a bird, the young female mites no doubt wander at random in search of a proper locus of attachment. They may even seek temporary shelter in certain protected areas, which explains why they often occur without eggs in the parascutellar grooves of the thorax. Thirty-five North American *Ornithomyia fringillina* bearing mite and egg clusters gave the following results: clusters on basal under side of both wings only, 21; on basal under side of one wing only, 7; on basal under side of one wing and on abdomen, 2; on abdomen only, 5. I suggest that mite clusters are restricted on the wings to the under side due to the repeated cleaning of the upper surface of wings and body with the fly's legs, which may also account for the scarcity or absence of clusters on the dorsum of the thorax. I have noted that young, non-gravid and unengorged female mites are sometimes found on the basal upper side of the wings, presumably before they are brushed off by the fly.

Thompson (1936b, p. 319) reports that a female *Ornithomyia fringillina*, from *Anthus pratensis*, at Skokholm Id., Wales, carried a female mite, surrounded by a mass of eggs, on the basal under side of each wing. The mite was referred by Vitzthum to his *Microlichus uncus*, and, if this identification is correct, the species is not restricted to *O. biloba*.

Büttiker (1948; 1949, p. 76, figs. 3-4, mislabelled *O. avicularia*) records and figures mite clusters, which he refers to *Microlichus uncus*, fixed to the basal veins on the under side of the wing of an *Ornithomyia biloba*, taken from *Hirundo rustica* at Langenthal, Switzerland. On the other hand, the same author (1949, p. 75, fig. 1) refers to *Pterolichus aquilinum* (a feather mite of the family Dermoglyphidae) mites from 4 *Ornithomyia avicularia* on *Buteo buteo*, in Switzerland: one fly, from Gnosca (Canton Tessin), carried a single larval mite on the hind femur; 3 others, from Zurich, carried 4 female mites with eggs on the wing veins, in the same position as the mite clusters of *M. uncus* on *O. biloba*. Nothing further is known of the association of *Pterolichus* with hippoboscids.¹²

¹² I cannot refrain from suspecting that these so-called "*Pterolichus aquilinum*" were misidentified and that the four flies from *Buteo buteo* were infested with *Microlichus*, like those from *Hirundo rustica*. The size given for the mite attached to the leg (ca. 1 mm.) is too large for a larva of a feather mite. The figure of the supposed larva could well be that of a gravid female *Microlichus* with the usual very short and thick first pair of legs of that genus more or less hidden.

Johnsen (1948, pp. 288 and 290), in Denmark, refers doubtfully to *M. uncus* mites surrounded by eggs, particularly at the under side of the wing of several *Ornithomyia avicularia* from a rook, *Corvus frugilegus*, and of 3 *O. fringillina* from unknown hosts.

Ash (1952, p. 30) states that, according to identifications he received from T. Hughes, *M. uncus* occurred in 1950 at Sunninghill, Berkshire, England, on both *Ornithomyia avicularia* and *O. fringillina*, and *M. avus* on *O. avicularia* only; but, in material taken the same year in Sweden, both species of mites were found together on each of these flies. R. Edwards (1951) refers mites found in England on *O. fringillina*, from wheatear, *Oenanthe oenanthe*, rock pipit, *Anthus spinoletta*, English sparrow, *Passer domesticus*, and starling, *Sturnus vulgaris*, to both *M. uncus* and *M. avus*. These flies were obtained at the Fair Isle Bird Observatory near the Shetlands. Quite recently, Ash and Hughes (1952) discuss in detail the mites previously reported by Ash (1952) from England and Sweden, listing the bird hosts of the infested flies; they also comment upon some of the structures used to define the species of mites of bird-flies and Mallophaga.

Prior to Vitzthum's paper of 1934, all mites found on hippoboscids were referred to *Myialges* Sargent and Trouessart (1907). The type of this genus, *Myialges anchora* Sargent and Trouessart (1907), was first described and figured from female mites and larvae found on the pigeon-fly, *Pseudolynchia canariensis* (Macquart) (= *Lynchia maura* Bigot), in Algiers, the females surrounded by eggs being fixed to the head, thorax and abdomen. The species was later reported from the same host at Pietermaritzburg, Natal (Thompson, 1936b), in Southwest Africa (Reichert, 1939), in Mauritius (Thompson, 1936b), and in California (Herman, 1945). A. C. Oudemans (1935) published a revised illustrated description of the female and larval types. *M. anchora* was described again from the pigeon-fly, at Recife, Brazil, as *Myialges pseudolynchiae*, by de Figueiredo and Simões Barbosa (1944). It seems to be found wherever its fly host occurs, and even flies taken from wild bird hosts in the Old World are often infested. Sometimes it is very common. Of 31 *P. canariensis* (15♀ and 16♂) collected at random from domestic pigeons at Aba, Belgian Congo, 17 (9♀ and 8♂) carried female mites, a few without, but most of them with a cluster of eggs. The majority were fixed to the abdomen, but some also to the thorax, particularly on the prosternum between the fore coxae. In 5 flies a female mite, either with or without eggs, was attached to the base of the rostrum membrane, on the under side of the head.

Only one of the flies carried one mite cluster on the under side in the basal area of one wing, and it was also infested on the abdomen, thorax, and rostrum membrane. At Tucumán, Argentina, according to Dr. Schuurmans Stekhoven (*in litt.*, 1952), the percentage of mite-infested *P. canariensis* was about 18 per cent for the females and 12.5 per cent for the males in the most heavily parasitized lot; the mites were attached mostly either to the head at the base of the palpi or to the sides near the tip of the abdomen, occasionally also in the space between the thorax and the abdomen.

In the original description, Sergeant and Trouessart noted the absence of a caruncle or adhesive pad on the first pair of legs, the tarsus ending instead in a heavy, two-hooked, anchor-shaped claw, which fastens the mite in the fly's cuticle. As Dr. D. Furman pointed out to me (*in litt.*, 1952), the stalked eggs are fixed to the fly's cuticle by a thin base or plaque probably secreted by the female mite at the time the egg is voided. When removing egg clusters from a fly, this thin base is often removed intact.

Ferris (1928b) published some new figures and critical notes of *M. anchora*, based on specimens from three species of *Ornithoica*, *O. vicina* (Walker) in North America, and *O. pusilla* (Schiner) and *O. philippinensis* Ferris in the Philippines.¹³ Thompson (1936b) found 2 females with egg masses of *M. anchora* (as named by Vitzthum) fixed to the posterior lobes of the abdomen of a female *Ornithomyia fringillina*, from *Dryocopus m. martius*, in Esthonia; I recently confirmed the identification of these flies.

A second species of the genus, *Myialges caulotoon* Speiser (1907, pp. 9-10), was based on several female mites surrounded by eggs, found mostly on the abdomen and in one case also on a leg of 2 *Lynchia albipennis* (Say) (= *Olfersia ardeae* Macquart), from *Ardea purpurea*, in Tanganyika Territory (Kibonoto on Mt. Kilimanjaro and Tanga). It was not figured by the author. The eggs,

¹³ Originally Ferris (1928b) recorded *M. anchora* "from *Ornithoica confluenta* (= *O. promiscua*), Pasadena, California, and Puerto Princessa, Palawan, Philippine Islands, and from *O. philippinensis*, Mati, Davao, Mindanao, Philippine Islands." The first of these flies, from Pasadena, was what I call *Ornithoica vicina* (Walker). The second, from Puerto Princessa, was later referred to *O. pusilla* (Schiner) by Ferris (1929, p. 284). As for *O. philippinensis* Ferris, it appears to be a peculiar species, to be discussed in Part II of the present work. Ferris did not give the bird hosts of the infested flies.

several dozen in each mass, were placed upright and fixed by a long, very thin, hyaline, stiff but curved stalk to the integument of the fly. Ferris (1928*b*) redescribed and figured as *M. caulotoon* females surrounded by eggs, found mostly on the abdomen, in one case also on the thorax, of *Ornithoica pusilla* (Schiner) (cited as *O. confluenta*) and *O. philippinensis* Ferris from the Philippines, the same flies also carrying mites referred to *M. anchora*, as mentioned before. But he was not certain that the mites were correctly named and even doubted that they were two distinct species. He voiced the suspicion that "actually the two forms have some connection with each other" and that "one is simply a developmental form of the other." E. P. Reed (1932) recorded *Myialges caulotoon* (from Ewing's identification) on several *Ornithomyia remota* Walker (as *O. chilensis* Reed, a synonym), at Valparaiso, Chile, from unknown bird hosts. Spencer (1928; 1938), Thompson (1936*b*) and I (1933*e*; 1935*a*) referred to the genus *Myialges* mites from several other bird-flies. Mention should also be made of mites found by Shipley (1911, 1, p. 360) on 3 *Ornithomyia fringillina* (as *O. lagopodis*) from red grouse, *Lagopus scoticus*, in England. These Waterston referred to the genus *Canestrinia*, but doubtless they were either *Microlichus* or *Myialges*. Edwards (1952) reports from the Fair Isle Bird Observatory near the Shetlands an *Ornithomyia avicularia*, taken on a twite, *Carduelis flavirostris*, and carrying on the abdomen several mite clusters tentatively referred to *Myialges*.

Thompson (1936*b*, p. 316) reported mites, similar to those of the bird-flies, fixed to biting lice (Mallophaga) from wild ducks (Anatidae) in Uganda; Vitzthum referred these to *Myialges caulotoon*. Later (1939) he observed such mites also on lice from Anatidae of North America and Ceylon, and published some excellent photographs of the infestations. Cooreman (1944) proposed for mites fixed to biting lice from a wild duck, *Mergus merganser*, in Belgium, a new genus *Myialgopsis*, with *Myialgopsis trinotoni* Cooreman as the type, said to differ from *Myialges* in the presence of a tarsal caruncle on the first pair of legs. According to Radford (1949), Thompson's supposed *Myialges caulotoon*, from lice on Anatidae, were likewise *Myialgopsis trinotoni*. However, the presence or absence of a tarsal caruncle appears to be an unreliable character, so that *Myialgopsis* is perhaps not generically separable from *Myialges*.

From the point of view of the life-history and ecology of the mites, the true relationship of those of the Hippoboscidae and of

the Mallophaga and their correct place in the general classification of the Acarina are of great importance. Sergent and Trouessart (1907) originally placed *Myialges* in the family Sarcoptidae; but, as now defined, the Sarcoptidae always have a pair of anterior vertical setae on the dorsal propodosoma (Baker and Wharton, 1952, p. 362), which setae are lacking in *Myialges*. At one time, Vitzthum (1934, pp. 12-13) regarded *Microlichus* and *Myialges* as closely related and was even doubtful about their being generically distinct. In his later comprehensive work on the Acarina (1942, pp. 890 and 898), however, he placed them in two different families: *Myialges* in the Myialgesidae and *Microlichus* in the Epidermoptidae. The Myialgesidae, which he said are "parasitic on Hippoboscidae, exceptionally on Mallophaga," were characterized by the tarsi of the first pair of legs lacking caruncles, which are present only on the second, third and fourth pairs. On the other hand, he stated that the Epidermoptidae live "on the skin of birds" and have caruncles on all four pairs of tarsi. In their recent "*Introduction to Acarology*," Baker and Wharton (1952, pp. 324, 369 and 374) follow Vitzthum's classification. However, they include in the Myialgesidae Cooreman's genus *Myialgopsis*, although it was defined by the presence of caruncles on the first pair of tarsi.¹⁴

The presence or absence of a caruncle (adhesive pad or ambulacrum) on the tarsi of the first legs is a fictitious character. Vitzthum (1934, p. 13) at first suspected that the caruncle might have been merely overlooked in *Myialges*; while Cooreman (1944, p. 3) suggested that the caruncle may be fugacious, being present in the newly-emerged female and lost after the mite anchors in the cuticle. That the caruncle is occasionally present on all four pairs of tarsi in *Myialges anchora* of the pigeon-fly, was recently observed by Dr. D. P. Furman (*in litt.*, 1952). *Myialges*, *Myialgopsis*, and *Microlichus* may therefore all be included in the Epidermoptidae and the family Myialgesidae should be dropped. Moreover, the remaining differences between these three so-called genera are very weak and perhaps not of more than specific value, in which case all the mites found attached to Hippoboscidae and Mallophaga could

¹⁴ Vitzthum (1942, p. 890) and Baker and Wharton (1952, p. 369) credit the family name Myialgesidae to Trouessart, 1907; but Trouessart did not place *Myialges* in a distinct family nor propose the family name, which dates from Vitzthum, 1942. It may be added that Cooreman (1944) proposed, "at least provisionally," an additional family Myialgopsidae for *Myialgopsis*.

be placed in the one genus *Microlichus*. It is fairly certain that several species of mites are involved; how many of those now described are valid cannot be decided from the available evidence.

With the relationships of the mites of the Hippoboscidae somewhat clarified, it becomes more probable that in all of them the major part of the life-history proceeds on or in the skin of birds, which normally harbor the larvae after they leave the fly, the several nymphal stages and the newly emerged adults of both sexes. After mating on the bird, some or possibly all females migrate to Hippoboscidae, where they attach to the integument, become fully gravid and eventually oviposit, the eggs clustering around the mother mite. After hatching from the egg, the mite larva probably returns to a bird before starting to feed. In this manner a fly infested with mites may transfer larvae to a new bird, particularly to nestlings, and this may possibly be the normal mode of dispersal of most species of *Microlichus*. If this view is correct, *Microlichus* should be included among the few cases of true hyperparasitism known among the Acarina.

While the female mites are not merely "riders," but undoubtedly true parasites, since they extract nourishment from the body fluids of the fly, it is difficult to estimate the damage they do to the insect. Ferris (1928*b*) called attention to the peculiar scars formed where the mites are fixed to the integument. Mr. K. W. MacArthur (*in litt.*, 1951) also noted these strongly sclerotized scars produced by the mites, which persist even after prolonged treatment with potash. They may be seen in a photograph of the tip of the abdomen of *Ornithomyia fringillina* received from Mr. MacArthur and published here with his permission (Fig. 19). Heavy infestation, particularly when the wings carry many egg clusters, might also impair flight by the mere weight of the parasites.

Often a substantial proportion of the general bird-fly population is mite-infested. For instance, during the summer of 1951, at the Fair Isle Bird Observatory near the Shetlands, according to Edwards (1952), mites were found on 47 of 362 specimens, or 13 per cent, of *Ornithomyia* (mostly *O. fringillina*) taken from 165 birds of 4 species.

The following partial list of New World Hippoboscidae observed carrying mites, probably all referable to the genus *Microlichus*, could be considerably extended. The term "mite cluster" is here used for a female mite surrounded by her eggs. The generic and specific names of the mites are retained as given by the several authors cited, although eventually they will probably all be placed

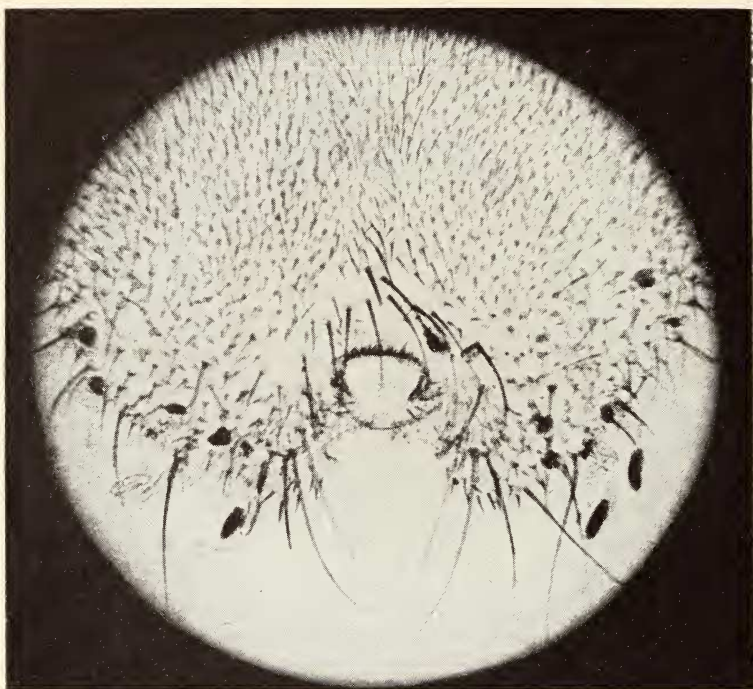


FIG. 19. *Ornithomyia fringillina* Curtis, female from Demarest, New Jersey, on *Dumetella carolinensis*. Cleared tip of abdomen with gravid female mites attached, showing the sclerotized scars made by the mites. Photograph by Mr. K. MacArthur.

in the genus *Microlichus*. The list now contains mite infestations on 20 American species of flies belonging to 8 genera. It shows that these parasites occur everywhere, in temperate as well as in tropical areas, and on many flies from a variety of bird hosts. Their prevalence strongly suggests that in most species of *Microlichus* preliminary feeding of the female on bird-flies, followed by oviposition on the insect, is a regular and essential feature of the mite's life-history. If so, the flies should be regarded as required intermediate hosts as well as carriers of the mites, and a normal link in their life cycle.

A. *Ornithoica vicina* (Walker) (= *O. confluenta* of authors, not of Say).

1. Ferris (1928*b*, p. 139) referred to *Myialges anchora* mites attached to the abdomen of a fly (cited as *O. confluenta*) from an unknown host at Pasadena, California.

2. Herman (1937*b*, p. 165) mentions mites attached to a fly (cited as *O. confluenta*) at North Eastham, Massachusetts; host unknown.

3. Female on *Pipilo fuscus falcifer*, from Berkeley, California, with a mite cluster on the under side of a vein in the basal third of the wing.

4. Fly from Valparaiso, Chile, on unknown host, with several mite clusters.

5. Female on *Buteo magnirostris*, from Juquia, State of São Paulo, Brazil, with several mite clusters.

6. Female on juvenile *Turdus m. migratorius*, from Demarest, New Jersey, with one large mite cluster at the right side of the tip of the abdomen.

7. Two females from near Valparaiso, Chile, on "zorzal," *Turdus magellanicus*, in the E. P. Reed Collection, carried mite clusters at the side of the dorsum of the abdomen, one on one fly, two on the other.

8. Out of a total of 29 flies collected from 6 *Junco phaeonotus dorsalis*, near Flagstaff, Arizona, by Mr. A. R. Phillips, 5 females (from 2 birds) carried mites, all attached to the veins on the under side of one or both wings; some of the mites were surrounded by eggs, others not.

9. Among 7 flies taken from young domestic fowl by S. L. Yoder at Annandale, Virginia, one female carried 2 mite clusters on the sides of the abdomen, one near the tip on the right side, the other about mid-length on the left side.

10. Female on English sparrow, *Passer domesticus* (introduced

from Europe), taken by Dr. C. M. Herman at Silver Spring, Maryland, with one mite cluster on the under side of the right wing, fixed to the vein closing the base of the anal cell.

B. *Ornithomyia fringillina* Curtis.

1. Female on *Pipilo fuscus falcifer*, from Berkeley, California, with several mite clusters on the dorsum of the abdomen. An *Ornithoica vicina*, taken from the same individual bird, was also infested with mites, as recorded above.

2. G. J. Spencer (1928, p. 257) reports mite clusters in the basal area of both wings of a fly taken on *Cyanocitta s. stelleri* at Tofino, Vancouver Id. Cooreman (1944, p. 8) lists the mite of this case under *Microlichus*, a generic name which Spencer did not mention, however. The same fly (called *Ornithomyia avicularia* by Spencer) carried also 16 Mallophaga.

3. G. J. Spencer (1938, p. 43) mentions a mite cluster, supposedly of *Myialges* sp., on a female from a hawk, at Jesmond, British Columbia, fixed to the tip of the abdomen.

4. G. J. Spencer (1938, p. 43) reports several clusters, supposedly of *Myialges* sp., on a fly from *Acridothores cristatellus* (introduced from the Far East, now feral in British Columbia), at Vancouver, fixed on the dorsum of the abdomen.

5. Female on *Dumetella carolinensis*, from Demarest, New Jersey, with several mite clusters attached to the hind margin of the abdomen. The scars made by the mites are shown in Fig. 19.

6. Female on *Hylocichla mustelina*, from Demarest, New Jersey, with several mite clusters on the under side of the basal area of both wings. This fly also carried 2 Mallophaga.

7. Female on *Zonotrichia albicollis*, from Demarest, New Jersey, heavily infested with at least 7 egg-laying mites, along the entire periphery at the sides of the abdomen.

8. Female on *Pipilo e. erythrophthalmus*, from Demarest, New Jersey, with one mite cluster at the under side of the basal area of each wing.

9. Female on *Geothlypis trichas brachidactyla*, from East Westmoreland, New Hampshire, with mite clusters in both wings.

10. Female on *Geothlypis trichas brachidactyla*, from Demarest, New Jersey, with one small mite cluster in the basal area of the left wing, on the under side.

11. Female on *Molothrus a. ater*, from Demarest, New Jersey, with one small mite cluster in the basal area of the right wing, on the under side.

12. Male on *Cyanocitta c. cristata*, from Demarest, New Jersey,

with a small mite cluster on the under side of each wing, in the basal area.

13. Female on *Dumetella carolinensis*, from Demarest, New Jersey, with one mite cluster in the basal area of the right wing, on the under side.

14. Male on *Dumetella carolinensis*, from Demarest, New Jersey, with several small mite clusters on the under side of each wing in the basal area.

15. Female on *Hylocichla mustelina*, from Demarest, New Jersey, with 2 mite clusters in the basal area of the left wing, on the under side.

16. Female on *Melospiza m. melodia*, from Barre, Vermont, with one mite cluster in the basal area of the left wing, on the under side, and another on the left side near the tip of the abdomen.

17. Male on *Hylocichla mustelina*, from Demarest, New Jersey, with a few non-gravid female mites, without eggs, near the base on the upper side of both wings.

18. Male on *Icterus galbula*, from Demarest, New Jersey, with one mite cluster in the basal area of each wing, on the under side.

19. Male on *Icterus galbula*, from Demarest, New Jersey, with several mite clusters in the basal area of each wing on the under side.

20. Male on *Hedymeles ludovicianus*, from Demarest, New Jersey, with several non-gravid female mites, without eggs, on various areas of the wings, thorax and abdomen; 3 of the mites in the left parascutellar groove.

21. Female on *Icterus galbula*, from Demarest, New Jersey, with several non-gravid female mites, without eggs, on various areas of the thorax and on the upper side in the base of the wing.

22. Female on *Melospiza m. melodia*, from Demarest, New Jersey, with several mite clusters in the basal area of both wings, on the under side.

23. Female on *Dumetella carolinensis*, from Demarest, New Jersey, with a few non-gravid female mites, without eggs, scattered over the body and apparently not attached.

24. Male on *Dumetella carolinensis*, from Demarest, New Jersey, with mites as in 23.

25. Female on *Dumetella carolinensis*, from Demarest, New Jersey, with mites as in 23.

26. Female on *Dumetella carolinensis*, from Demarest, New Jersey, with several non-gravid female mites, without eggs, wedged in the parascutellar grooves, on both sides.

27. Female on *Pipilo e. erythrophthalmus*, from Demarest, New Jersey, with mite clusters on the under side in the basal area of both wings, one in one wing, two in the other.

28. Female on *Toxostoma rufum*, from Demarest, New Jersey, with 2 mite clusters on the under side in the basal area of the right wing, and a few non-gravid female mites, without eggs, in both parascutellar grooves.

29. Male on *Pipilo e. erythrophthalmus*, from Demarest, New Jersey, with only non-gravid female mites, without eggs, a few on the basal area at the under side of both wings and several in both parascutellar grooves.

30. Male without host, from Barre, Vermont, with 2 mite clusters on the under side in the basal area of the right wing and 3 clusters on the abdomen.

31. Female on *Hylocichla mustelina*, from Demarest, New Jersey, with one mite cluster on the under side in the basal area of the right wing.

32. Male without host, from Barre, Vermont, with several non-gravid females, without eggs, in the basal area of the upper and under side of the left wing.

33. Female on *Icterus galbula*, from Demarest, New Jersey, with several non-gravid females, without eggs, in various areas of the abdomen and a few on the under side of the basal area of both wings.

34. Male on *Icterus galbula*, from Demarest, New Jersey, with several non-gravid females, without eggs, in various areas of the body, particularly in the parascutellar grooves, and a few on the upper surface in the basal area of both wings.

35. Male on *Dumetella carolinensis*, from Demarest, New Jersey, with many non-gravid female mites, without eggs, in various areas of the body and a few in the basal area on the upper side of both wings.

36. Female on *Quiscalus q. quiscula*, from Pequannock, New Jersey, with many non-gravid female mites, without eggs, most of them flattened against the integument and closely packed together on the back of the left side of the abdomen.

37. Male on *Dendragapus obscurus fuliginosus*, from Kamloops, British Columbia, with 2 mite clusters on the dorsum of the abdomen.

38. Male on *Ixoreus n. naevius*, from Trinity Valley, Vernon, British Columbia, with mite clusters in the basal area on the under side of both wings, 1 in one wing, 2 in the other.

39. Female on *Bonasa umbellus umbelloides*, from Okanagan Landing, British Columbia, with several mite clusters in the basal area on the under side of both wings.

40. Female on *Hylocichla guttata faxoni*, from Mt. Desert Island, Maine, with mite clusters on the under side in the basal area of both wings.

41. Female on *Molothrus a. ater*, from Old Deerfield, Massachusetts, with mite clusters on the under side in the basal area of the left wing.

42. Female on *Dendragapus obscurus richardsoni*, from Bridger Mountains, Montana, with several mite clusters on the under side in the basal area of both wings.

43. Female on *Zonotrichia albicollis*, from Columbus, Ohio, with mite clusters on the under side in the basal area of both wings, 4 in one wing, 2 in the other.

In this species of *Ornithomyia*, when female mites with egg clusters are present on the wings, they are always fixed to the veins surrounding the basal and anal cells and on the under side. The foregoing list records infested flies from 20 different species of birds (16 Passeriformes, 3 Galliformes and 1 Falconiformes). The rate of infestation seems to vary from year to year and is presumably correlated with similar variations of the mite infestation of the bird population. In the summer and fall of 1950 mite infestation was unusually low on the flies at Demarest, New Jersey, only 2 being infested among 46 *fringillina* taken by Mr. B. S. Bowdish on 37 passerine birds of 14 species, all trapped alive.

C. *Ornithomyia remota* Walker. As mentioned before, E. P. Reed (1932) recorded an infestation of *Myialges caulotoon* on a fly of this species in Chile.

1. Three females on *Nesocichla eremita gordonii*, from Inaccessible Id., Tristan da Cunha Group, each with several mite clusters on the under side of the veins in the basal areas of both wings.

D. *Stilbometopa podopostyla* Speiser:

1. A female on *Leptotila verreauxi decipiens*, from Barra do Tibagi, Rio Parapanema, State of São Paulo, Brazil, carried small mite clusters on the hind part of the thorax, to the side of the scutellum.

Herman (1945, p. 24) noted that among several hundred specimens of *Stilbometopa impressa* (Bigot), a common fly on *Lophortyx californica vallicola* in California, he never found one with mites, while they were not uncommon on *Lynchia hirsuta* taken on the

same host. Mr. I. B. Tarshis (*in litt.*, 1951) confirmed this for both flies from his own observations.

E. *Ornithoctona erythrocephala* (Leach).

1. Two females on *Oreopeleia linearis infusca*, from Vista Nieve, Sa. Marta, Colombia, each with mite clusters on the abdomen, mostly near the tip; one cluster ventrally near the base.

2. Four females on one *Accipiter s. velox*, from Whitefish Pt., Michigan, with mite clusters on the dorsum of the abdomen; the dorsum of one fly was nearly covered with them.

3. Female on a species of *Falco*, from Hansa near Humboldt, Sa. Catharina, Brazil, with 6 female mites, some of them with a few eggs, on the dorsal side of the abdomen.

F. *Ornithoctona fusciventris* (Wiedemann).

1. Two females on *Calospiza arthus aurulenta*, from Virolin, Santander, Colombia, with mite clusters on the thorax, chiefly wedged in the deep parascutellar grooves; one of the flies also with a cluster on the sternum, in the notch between the prosternal lobes, and with another cluster on the under side of the articulation of a wing.

G. *Lynchia albipennis* (Say).

1. Female on *Botaurus lentiginosus*, from St. Paul, Minnesota, heavily infested. In addition to 2 large clusters on the under side of the basal area of the left wing, 4 clusters on both side margins of the abdomen, some females starting to oviposit on the dorsum of the abdomen, and one female with a few eggs on the anterior face of the right fore femur.

2. Male on *Botaurus lentiginosus*, from Patterson Lake, Michigan, with 4 mites: one with one egg on the under side in the basal area of the right wing; one without eggs on the left side near the tip of the abdomen; one without eggs on the left mid femur; and one with a few eggs on the gula of the head.

3. Female on *Botaurus lentiginosus*, from Bald Eagle Lake, Minnesota, very heavily infested. This fly was briefly mentioned by MacArthur (1948, p. 387). Nearly all the clusters on the abdomen, the wings being entirely free from mites. Seven females with egg masses on the venter, 4 of them in the basal median area; at least 9 more females, mostly imbedded in large clusters of eggs at the sides of the dorsum, 2 females as yet without eggs. In addition one female, without eggs, fixed to the integument of the right fore femur.

4. Two females on *Botaurus lentiginosus*, from Racine, Wisconsin, each with several mite clusters.

5. Male on *Botaurus lentiginosus*, from Philadelphia Neck, Pennsylvania, with mite clusters.

It seems remarkable that 5 specimens of this common fly observed carrying mites, were taken on *Botaurus lentiginosus*.

6. Female from an unknown host at Iowa City, Iowa, with 3 large mite clusters on the dorsal sides of the abdomen and one small cluster on the under side of the base of the left wing.

H. *Lynchia angustifrons* van der Wulp.

1. A female fly on *Accipiter s. velox*, from Vineland, Ontario, May 13, 1924, is the most heavily infested hippoboscid I have observed. Both upper and under surfaces of the abdomen are nearly completely covered with crowded mite clusters. It is impossible to determine exactly how many females deposited the eggs, but they numbered at least fifty and the eggs run into the hundreds. In addition, there is a large mite cluster on the head, attached beneath the base of the palpi, in such a way that it would seem the fly was eventually unable to feed. The wings, thorax and legs, however, are entirely free of mites.

I. *Lynchia nigra* (Perty).

1. Three females on *Buteo jamaicensis borealis*, from Grindrod, British Columbia, each with a single female mite, without eggs, on one side of the abdomen.

2. Female on *Accipiter bicolor pileatus*, from Fazenda Recreio, Coxim, Matto Grosso, Brazil, with one mite cluster on the right side at the hind third of the abdomen.

3. Male on *Milvago c. chimachima*, from Rio das Mortes, Posto Pindaiba, Matto Grosso, Brazil, with 3 mite clusters on the sides and venter of the abdomen, a small group at the under side in the basal area of one wing, and a large cluster on the right hind tibia.

4. Female on *Buteo jamaicensis calurus*, from Tucson, Arizona, April 5, 1916, with a gravid female mite, without eggs, fixed on the dorsal left side of the abdomen.

5. Female on *Cathartes a. aura*, from east of Tucson, Arizona, May 23, 1949 (A. R. Phillips), with 2 female mites fixed on the right mid femur, one without and the other with eggs.

J. *Lynchia fusca* (Macquart).

Herman (1945, p. 23) states that he saw mite clusters on several specimens from hawks and owls in California. He has sent me more definite information on the following two cases.

1. Eleven flies on one *Bubo virginianus* subsp., from Napa Co., were all infested; but flies emerging from 7 puparia deposited by these infested flies, were free of mites. The clusters usually con-

sisted each of a female mite surrounded by a large mass of eggs, and were fixed to the under side of the wing veins and to the venter of the abdomen near the tip. See fig. 12 in Herman's paper.

2. Two males and 6 females among 19 flies on one *Bubo virginianus* subsp., from Lassen Co., were infested with mites.

3. Two flies on *Otus asio floridanus*, from Auburn, Alabama, with several mite clusters on the dorsum of the abdomen.

4. Two females on an unknown host, from Ipiranga, State of São Paulo, Brazil, each with 2 mite clusters on the abdomen, dorsally on one fly and ventrally on the other.

5. One male and one female on *Tyto alba tuidara*, from Ipiranga, State of São Paulo, Brazil, with mite clusters on the dorsum of the abdomen, 8 on the male and 5 on the female.

6. Female from an unknown host, from Monte Alegre, State of São Paulo, Brazil, with 4 mite clusters on the sides of the abdomen.

K. *Lynchia hirsuta* Ferris.

1. Herman (1945, p. 23) reports seeing mite clusters on one of 11 flies on *Lophortyx californica vallicola*, in California. He writes me that he examined since 36 more of these flies without finding mites.

2. Mr. I. B. Tarshis (*in litt.*, 1951) observed mites on about a dozen flies on *Lophortyx californica vallicola*, from various Californian localities.

3. One female and 3 males on *Lophortyx californica*, from the Hastings Natural History Reservation near Jamesburg, Monterey Co., California, each with from 1 to 3 mite clusters on the abdomen.

Mr. Tarshis informs that at the Hunter Liggett Military Reservation, San Benito Co., California, about 2.2 per cent of some 900 *L. hirsuta*, taken from *L. c. vallicola*, were infested with mites.

L. *Pseudolynchia canariensis* (Macquart) (= *Lynchia maura* Bigot). It may be of interest that one of Macquart's two cotypes of *canariensis*, from the Canary Islands, now at the Paris Museum, carries 6 mite clusters on the hind part of the abdomen (J. Bequaert, 1935a, p. 399).

1. I have mentioned before *Myialges pseudolinchiae* de Figueredo and Simões Barbosa (1944), described from a fly on domestic pigeon at Recife, Brazil. I regard this mite as a synonym of *Myialges anchora*.

2. Fly on domestic pigeon, from Havana, Cuba, with mite clusters, according to Dr. J. Perez Vigueras (J. Bequaert, 1935a, p. 397).

3. Bishopp (1929b, p. 980) reports that mites, probably of the

genus *Myialges*, were attached in great numbers to some flies on domestic pigeons at Lockhart, Florida.

4. Dr. C. M. Herman informs me (*in litt.*, 1951) that 2 females out of a lot of 3 males and 2 females, on domestic pigeons, from San Francisco, California, were infested with mites.

5. Out of 5 flies taken on domestic pigeons, at Rio de Janeiro, Brazil, 3 females were infested with mites. The heaviest infestation consisted of 4 clusters on the sides and venter of the abdomen of one fly. The other 2 flies each had one cluster on the abdomen, and one of them carried besides a female mite, without eggs, on the rostrum membrane of the head.

6. A female on a domestic pigeon at Atlanta, Georgia, received from Mr. P. W. Fattig, carried one small mite cluster near the dorsal tip of the abdomen.

7. The high rate of mite infestation observed by Dr. J. C. Schuurmans Stekhoven and his co-workers at Tucumán, Argentina, was mentioned before.

8. Male from a domestic pigeon, at Ames, Iowa, August, 1929 (H. M. Harris), with 2 female mites on the abdomen: one non-gravid, dorso-laterally on the left side, some distance before the tip; the other with a large package of eggs on the right side near the tip; in this cluster only the female mite was attached to the integument, all the eggs being fixed to the venter of the mite, some of them being stalked and others sessile.

M. *Pseudolynchia brunnea* (Latreille).

1. Male on *Chordeiles m. minor*, from Ipiranga, State of São Paulo, Brazil, with several mite clusters on the basal veins at the under side of one wing.

N. *Microlynchia pusilla* (Speiser).

1. Dr. C. M. Herman (*in litt.*, 1951) found mites on a female on *Zenaidura macroura marginella*, from Brawley, California, collected by G. F. Augustson. This case was inadvertently referred by Herman (1945, p. 23) to *Pseudolynchia canariensis*, the author informs me.

O. *Microlynchia crypturelli* J. Bequaert.

1. Female on *Columba rufina sylvestris*, from Nova Teutonia, State of Santa Catharina, Brazil, with 2 small mite clusters on the thorax, one on each pleurotergite, immediately behind the base of the wing.

P. *Olfersia spinifera* (Leach).

1. Two flies on *Fregata minor ridgwayi*, from Tower Island, Galapagos: one fly with a female mite on the upper side of the first

longitudinal vein, close to the base of the left wing; the other fly with a female surrounded by many stalked eggs on the left mesopleuron, immediately behind the base of the fore leg. At one time (J. Bequaert, 1933e), I referred these mites to *Myialges*.

2. The male type of *Ornithomyia unicolor* Walker, a synonym of *O. spinifera*, from *Fregata magnificens rothschildi* in Jamaica, bears a mite cluster on the sides of the metathorax, immediately above the insertion of the right hind leg.

Q. *Olfersia fossulata* Macquart.

1. Thompson (1936b, p. 316) records a fly on *Pelecanus* sp., from South America, with one mite cluster, referred to *Myialges* sp., on the under side of the metathorax.

R. *Olfersia coriacea* van der Wulp.

1. Male on *Crax fasciolata*, from Goyaz, Brazil, with a single female mite, without eggs, fixed by the hypostome to the left side of the abdomen.

S. *Olfersia bisulcata* Macquart.

1. Male on *Coragyps atratus foetens*, from Rio Tapajos, State of Pará, Brazil; with one large mite cluster near the mid-dorsum of the abdomen.

T. *Olfersia fumipennis* (Sahlberg).

1. Female from British Honduras (Newman), on *Pandion haliaeetus carolinensis*, with a cluster of eggs and a female mite on the under side of the basal veins of the right wing and a gravid female mite without eggs on the right side of the metathorax below the insertion of the wing.

5. Parasitic Hymenoptera. The early instars of most Diptera are frequently destroyed by various parasitic Hymenoptera or more rarely by certain other Diptera. The Hippoboscidae are unusually free from such attacks, no doubt due chiefly to the very short duration of the extra-uterine development, the only time at which parasitic insects could oviposit in the newly-voided, soft-skinned larva before it hardens into a puparium. The fact that only single larvae are deposited at rather long intervals by the gravid female flies, which, moreover, usually scatter them at random or may even hide them, further decreases the parasite's chances of encountering them at the proper oviposition time. The few insects known to parasitize hippoboscid puparia are minute Hymenoptera, probably all of the group Chalcidoidea. None are specific or restricted to the Hippoboscidae, but they are instead polyphagous parasites with a wide host range.

Modeer (1785, p. 37), in Sweden, first mentioned that he bred

both sexes of an "ichneumon" (a term then used for all parasitic wasps) from several puparia of *Stenopteryx hirundinis* (= *Hippobosca hirundinis*). He stated that about 30 ferruginous wasps, a little larger than fleas, emerged from each puparium. They appeared early in August from puparia collected in swallows' nests the same spring, but only about mid-June of the next year from puparia taken in the autumn. Zetterstedt (1848, 7, p. 2909) suggested that Modeer's parasite might have been one of the Encyrtidae, although he did not see the specimens. It should be added that quite possibly Modeer bred his parasites from puparia of *Crataerina pallida* and not of *Stenopteryx hirundinis*, these two flies being commonly confused by the early entomologists. In any case, no insect parasites have since been obtained from *Stenopteryx*.

Cornelius (1869, p. 407) bred a "Pteromaline chalcid fly" from puparia of *Crataerina pallida* found in the fall in a nest of European swifts, *Apus apus*, near Eberfeld, Germany, the parasite emerging the next April; no further identification was attempted. Bagnall (1915) reared *C. pallida* from puparia in a swift's nest at Newcastle, England; but one of the puparia yielded instead a small chalcid. This was possibly the parasite which Waterston later found in Bagnall's collection and identified as *Mormoniella vitripennis* (Walker), according to Gahan (1927, p. 6); although Waterston stated, perhaps by an oversight, that the specimens had been "reared from a puparium of *Stenopteryx* found in a house-martin's nest." *M. vitripennis* (= *Nasonia brevicornis* Ashmead), one of the Pteromalidae, is a widespread parasite of many Diptera, particularly muscoids. Recently Mr. G. E. Woodroffe sent me some chalcids he bred from a puparium of *Crataerina pallida* in England. These were kindly identified by Dr. D. B. Burks, of the U. S. Bureau of Entomology and Plant Quarantine, as *Dibrachys cavus* (Walker), also one of the Pteromalidae and likewise a cosmopolitan parasite of a variety of insects in several orders.

Stadler (1948, p. 52) states incidentally that "an entirely yellow braconid" issued from a puparium of an undetermined *Ornithomyia* found in Germany in the nest of a sand martin, *Riparia riparia*. It is unfortunate that nothing more is known of this interesting parasite. The host was, I suspect, *Ornithomyia biloba*.

Schuermans Stekhoven and his co-workers, in Tucumán, Argentina, found 4 specimens of a chalcid in a puparium of the pigeon-fly, *Pseudolynchia canariensis* (unpublished observations). The parasites were identified by Dr. Luis De Santis, of the Museum of La Plata, as *Mormoniella vitripennis* (Walker).

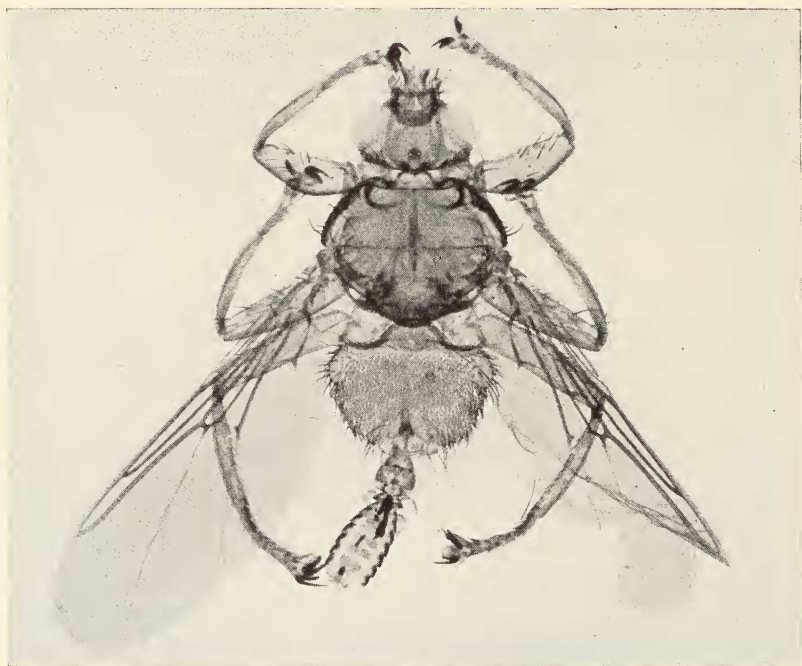


FIG. 20. *Ornithomyia fringillina* Curtis, male from Demarest, New Jersey, on *Dumetella carolinensis*, with Mallophagan attached. From MacArthur, 1948, fig. 233.

It is interesting to note that the only insect parasites of louse-flies which have been definitely identified are two cosmopolitan species of Pteromalidae with a wide range of hosts. Furthermore, they have been bred thus far only from species of bird-flies whose puparia are often abundant in the nesting sites of their hosts, swallows, martins, swifts and domestic pigeons, where many birds breed together. These factors tend to increase the local louse-fly population and particularly the number of larvae deposited in a relatively small area, thus favoring parasitism by polyphagous chalcid wasps.

Phoresy of Mallophaga. Certain Hippoboscidae of birds occasionally carry one or more biting (or chewing) lice (Mallophaga), attached by the mandibles to the integument, usually at the base of a body seta, more rarely to a vein of the wing.¹⁵ Such cases of so-called "phoresy" are on the border line of true parasitism. Each fly usually carries only one or two lice; exceptionally there may be more, respectively 15, 16 and even 31 in three observed cases. K. W. MacArthur (1948) mentions an *Ornithomyia fringillina*, from *Turdus m. migratorius*, with 8 lice placed close together in a semi-circle, along the sides of the abdomen, all heads pointing to the center of the circle. The lice often select the postero-lateral areas of the abdomen; and, if two lice are present, they may be placed more or less symmetrically, with the heads directed forward and the remainder of the bodies backward, flattened against the integument of the fly. Possibly the lice are more commonly seen attached to the abdomen because in other positions their hold is so precarious that they usually drop off before being noticed.

So many cases are now on record of biting lice being carried by bird-flies in all parts of the world, that this type of phoresy can no longer be regarded as abnormal, particularly in view of the fact that the Hippoboscidae are rarely collected in large numbers. Its significance and determining factors have been the subject of much speculation. The problem cannot be merely dismissed with the statement that the "Mallophaga which use Pupa to go from one bird to another" are cases of "phoresy due to a trophic stimulus" (Vachon, 1941, p. 12), as will appear from the subjoined discussion.

¹⁵ Throughout this account the term "lice" will refer only to "biting lice," the generally accepted English name for Mallophaga, but which Hopkins (1949, p. 388) wishes to replace by "chewing lice." There is no evidence that Anoplura ever attach to Hippoboscidae.

Observations by Clay and Meinertzhagen (1943), in England, seemed to lend some support to the view that lice might attach to a fly only after the bird host dies. They relate how on two occasions a single *Ornithomyia fringillina* (= *O. lagopodis*), free of Mallophaga, was taken on a freshly killed Shetland starling, *Sturnus vulgaris zetlandicus*, in the Orkneys. In each case the fly was returned to the dead host, which was chloroformed an hour later. The dead flies were then recovered bearing specimens of *Philopterus sturni* attached to the abdomen, 3 females in one case, 7 males and 21 females in the other. A few other similar experiments gave negative results, however. The one positive result seemed to agree with Harrison's (1913, p. 109) conclusion "that the mallophagous insects which find a hippoboscid upon the body of a dead host, fasten upon it, as its body temperature is above that of the defunct bird, without any intent, conscious or otherwise, of seeking transport to a new host. This would seem the more reasonable view to take, and it still allows the possibility of infection of a new host by parasites carried by a hippoboscid." Observations by bird-banders, who collect flies from living, healthy birds, do not support this explanation, however. Among 63 flies (46 *Ornithomyia fringillina* and 17 *Ornithoica vicina*) taken by B. S. Bowdish during the 1950 season, in New Jersey, on 50 birds belonging to 13 species, 5 carried Mallophaga (3 *O. fringillina* and 2 *O. vicina*). Ash (1952, p. 29), in England, likewise found that out of 108 *Ornithomyia avicularia* and *O. fringillina* taken from live birds, 7, or 6.5 per cent, all *O. fringillina*, carried lice. It is doubtful, therefore, that the main factor inducing lice to attach to a fly is associated with the death of the host or with the greater body heat of the fly, even though these may be sometimes added incentives. After the host dies, all ectoparasites possibly tend to congregate in a few areas of the bird's body which retain heat longer than others, thus increasing the chances of lice coming in contact with flies. Ewing (1927) offered some other possible explanations, none of them very satisfactory. He supposed, for instance, that bird-lice might attempt biting the integument of a fly in search of food, mistaking it for the bird's skin; or that they might be induced to attach by some peculiar scent emanating from the fly, by some attractive secretion of the fly's integument, or by the heat temporarily acquired by the fly's body while in contact with the skin under the protective layer of feathers. These and other suggestions may well be worth investigating; meanwhile the instinctive or environmental stimuli inducing the lice to attach remain uncertain.

The most attractive and purely teleological explanation of the phoresy of Hippoboscidae is, of course, that lice attach intentionally to the flies in order to obtain ready transportation to a new host, which would imply instinctive foresight on the part of the louse. Most naturalists will find it difficult to admit such purposeful behavior, obviously not induced by physiological or morphological peculiarities of either louse or fly. It would seem extremely doubtful that phoresy is now or could ever have been of sufficient benefit to the species of louse to have much survival value. It does not occur often enough to ensure transportation to a new host when needed, particularly in view of the very small proportion of birds of a given species harboring flies in the total bird population. The probability that a winged hippoboscid leaving a dead or live bird, away from the nest, might reach another bird suitable to the particular louse carried by the fly, is even smaller. As MacArthur (1948) points out, most species of Mallophaga are narrowly restricted in the choice of a host, while the majority of Hippoboscidae, and particularly most species of *Ornithomyia* and *Ornithoica*, show very little host specificity. The chances of a given species of louse reaching the proper host by fly transport appear therefore to be remote. Nevertheless, Miss Clay (1949, p. 293) considers it possible that transference by hippoboscid flies is one of the normal ways in which the cuckoo, *Cuculus canorus*, obtains its louse population, as except during copulation, there is no contact between individual cuckoos. I have difficulty in accepting this suggestion. It should also be noted that very few of the numerous species of biting lice occurring on birds have been observed using this supposed roundabout method of survival, most of them man-aging well without it.

All considered, it seems reasonable to regard the phoretic associations of lice and bird-flies as fortuitous, though rather frequent occurrences. Chance encounters of the parasites occur on the live bird when they seek out the same areas of the plumage, and on a dying bird when all parasites tend to congregate where more of the body heat is retained. It may be significant in this connection that most reported cases of phoresy are from flies on small or medium-sized birds, where different parasites have a better chance to meet. Possibly also the attachment of the louse to the fly is fortuitous, the louse merely grabbing the fly's setae with the mandibles, as it is wont to do with the barboles of the feathers.

There is no evidence that this type of phoresy is ever of any

benefit to the hippoboscid, which merely tolerates it, because the lice appear to do little if any harm and the fly has no means of keeping them off or removing them. There is also no proof that the lice obtain any nourishment from the flies.

No doubt a hippoboscid leaving a bird with one or more of the host's lice attached, reaches occasionally another bird, which will be usually of a different species. This might explain certain cases of so-called "straggling" or the occurrence in nature of species of Mallophaga on abnormal hosts. Recorded below is the capture on a vulture in Oregon of an *Ornithomyia fringillina*, normally not found on this type of bird, carrying a species of *Brüelia* characteristic of Fringillidae. Ash (1952, p. 29) reports a similar case in England of an *Ornithomyia avicularia* from a live great spotted woodpecker, *Dryobates major*, transporting *Brüelia marginata*, a specific louse of the European blackbird, *Turdus merula*. Miss Clay (1949, p. 293) discusses the possible rôle which phoresy by hippoboscids may have played in the speciation of the Mallophaga.

Very few of the lice observed on louse-flies have been named as to species or even genera, mainly owing to the present unsatisfactory state of mallophagan taxonomy. Guimarães (1944) reviewed critically 20 cases in which a specific identification of the louse was attempted. He found that in 11 of them the lice belonged to species known to occur normally on the bird species carrying the fly. The identification of the louse was obviously erroneous in one case; while in 4 cases the bird on which the flies were taken is unknown. The following additional cases, all from the Old World, should be added to Guimarães' list. Eichler (1939, p. 223) reports *Sturnidoecus sturni* on *Crataerina pallida* from *Apus apus*, *Philopterus pastoris* on *Ornithoeca metallica* from *Pastor roseus*, and *Brüelia merulensis* on *Ornithomyia avicularia* from *Cuculus c. canorus*. Clay and Meinertzhagen (1943) repeat 2 of Eichler's cases and add 3 more: *Brüelia glandarii* on *Ornithomyia avicularia* from *Garrulus glandarius rufitergum*, and *Sturnidoecus sturni* on *Ornithomyia fringillina* (= *O. lagopodis*) from *Sturnus vulgaris zetlandicus* (on 2 birds). Eichler (1946) has one more case of *Docophorulus lannii* on *Ornithomyia avicularia* from *Lanius collurio*. Ansari (1947) records the interesting occurrence of *Columbicola columbae* on *Pseudolynchia canariensis* from the wild rock pigeon, *Columba livia intermedia*, in the Punjab. Phoresy of *Brüelia glandarii* by *Ornithomyia avicularia* on *Garrulus g. glandarius* was reported by Callot (1946) from France and by Büttiker (1949, p. 75) from Finland. Ash (1952, p. 29) cites *Brüelia merulensis* on *Ornitho-*

myia avicularia from *Turdus merula* (on 3 birds; also recorded from this fly on the same host by Thompson, 1952b, p. 38), and *Brüelia marginata* on the same fly from *Dryobates major* and *Turdus merula*. Hopkins (1947, p. 170) mentions a species of *Hohorstiella* carried by an undetermined hippoboscoid from an unidentified dove, at Sterkfontein, Transvaal. It may be of some interest that, as Miss Clay (1949, p. 293) pointed out, all the Mallophaga found on hippoboscids and identified thus far, belong to the superfamily Ischnocera.

The following summary of the known cases of phoresy of lice by American Hippoboscidae includes all published and some new records. Unless the contrary is stated, I have personally examined the flies of those previously published, correcting the identifications if needed.

A. *Ornithoica vicina* (Walker). This is the species generally called *O. confluenta* in American literature (see Part II for a discussion of the nomenclature). Although it is nearly as common on North American birds as *Ornithomyia fringillina*, it is more rarely taken carrying lice, probably because the fly's small size makes it difficult for a louse to grasp it.

1 and 2. The first two cases of phoresy for *O. vicina* were recorded by Clay and Meinertzhagen (1943; as *Ornithoica confluenta* and *Ornithomyia confluenta*), from California. The more precise localities are added here from my own records. A fly from Pasadena, on *Aphelocoma c. californica*, carried a female louse of the genus *Brüelia*, attached to a vein of the wing.¹⁶ As shown in the authors' illustration, one mandible of the louse was beneath the junction of the costa and first longitudinal, pressing the latter upwards against the other mandible which had pierced the wing membrane from above. The second fly, from Altadena, on *Pipilo maculatus megalonyx*, also carried a female *Brüelia* sp. fixed on a vein of the wing.

3 and 4. B. S. Bowdish collected the following two flies from living, trapped birds at Demarest, New Jersey, in 1950. A male fly on *Turdus m. migratorius*, August 6, had one louse attached. Another male fly on *Cyanocitta c. cristata*, August 2, carried 3 lice, one fixed to the wing and the others to the abdomen.

5 and 6. Two flies on a "thrush," taken by W. Clarke-MacIntyre, at Abitagua, Ecuador, each carried a mallophagan.

¹⁶ The correct generic name for most of the biting lice formerly recorded as *Degeeriella* appears to be *Brüelia*.

7 to 9. Three flies from Nova Teutonia, Santa Catharina, Brazil, taken by F. Plaumann on *Uroleuca cristatella*, each carried a louse on the abdomen.

10. One fly from Nova Teutonia, Santa Catharina, Brazil, taken by F. Plaumann on *Pyroderus scutatus*, had a louse attached to the tip of the abdomen.

B. *Ornithomyia fringillina* Curtis. By far the largest number of known North American cases, 42 out of total of 69, are from this species, the flies being taken on 18 species of birds (Passeriformes with 2 exceptions). Thirty of the cases I observed myself among some 500 *O. fringillina* seen from North America, about 6 per cent of the flies carrying lice, the normal percentage for this type of phoresy. In the Old World also the majority of the reported cases are from either of the two common species of *Ornithomyia*, *O. avicularia* and *O. fringillina*. The first observation of the kind, by C. Aubé (1857) concerned an undetermined species of *Ornithomyia*, from a magpie, *Pica p. pica*, in France, which carried 2 "lice." Thompson (1947) noted that of 112 *O. avicularia* collected from trapped birds by one bird-bander in the same British locality, 11, or roughly 10 per cent, had lice attached. Ash (1952, p. 29), also in England, found that of 108 *O. avicularia* and *O. fringillina* collected from trapped birds in one season, 7 *O. avicularia*, or 6.5 per cent, bore lice. The proportion was even lower in a collection of 46 *O. fringillina* taken from live trapped birds at Demarest, New Jersey, by Mr. B. S. Bowdish in 1950, only 2, or less than 5 per cent carrying lice. According to Edwards (1952), during the summer of 1951 phoresy was unusually common on *Ornithomyia fringillina* taken from live starlings, *Sturnus vulgaris*, at the Fair Isle Bird Observatory near the Shetlands, 17 of 78 flies, or 21.8 per cent, carrying lice; it was, however, very rare on flies taken from wheat-ear, *Oenanthe oenanthe* (only on 1 of 205 flies), and not seen on flies from other birds.

1. N. Banks (1920) reported the first known case of phoresy of lice for an American hippoboscid. A male *Ornithomyia*, later referred to *O. anchineuria* (a synonym of *O. fringillina*) by Johnson (1922), from *Perisoreus canadensis*, carried 2 lice, one on each side near the tip of the abdomen. (The supposed new species, *Perisoreus barbouri*, was never described.) Thompson (1937) determined the 2 lice as females of a species of *Brüelia*.

2 and 3. W. L. McAtee (1922) reported 2 cases. One louse, later identified by Ewing (1927) as *Brüelia rotundata* (Osborn), was attached by the mandibles to the upper right surface at the tip

of the abdomen of a female fly from an unknown bird, collected at the mouth of the Macfarlane River, Lake Athabaska, Saskatchewan, by F. Harper, Aug. 11, 1920. Another specimen of *Brüelia rotundata* was fixed in the same manner on a fly from *Corvus brachyrhynchos hesperis*, at Ontario, Oregon.

4 and 5. H. E. Ewing (1927) added 2 more cases. A fly on *Melospiza m. melodia*, from Gates Mills, Ohio, carried a male and a female of *Brüelia interposita* (Kellogg), placed symmetrically at the sides near the tip of the abdomen. Another fly from the same locality, on *Dumetella carolinensis*, had a single *Brüelia interposita*. Ewing published a photograph of this case. He called the flies *Ornithomyia avicularia*; although I have not seen them, there can be little doubt that they were the common North American species, *O. fringillina*.

6. G. J. Spencer (1928) found a fly on *Cyanocitta s. stelleri*, at Tofino, British Columbia, carrying 16 *Brüelia deficiens* (Piaget), attached by the mandibles to the abdominal tergites. Spencer records the fly as *O. avicularia*; although I have not seen it, I refer it to *O. fringillina*.

7 and 8. G. B. Thompson (1936) recorded 2 female *Brüelia* sp. attached to the terminal segment of the abdomen of a male fly on *Melospiza m. melodia*, on Martha's Vineyard, Massachusetts; also 2 females of *Brüelia simplex* (Kellogg) fixed to the dorsal surface of the abdomen of a female fly on *Turdus m. migratorius*, at Elmhurst, New York.

9 and 10. G. B. Thompson (1937) reported 2 more cases: a fly on *Hylocichla u. ustulata*, at Vancouver, British Columbia, carrying 4 female and 1 immature *Brüelia interposita* (same specimen recorded by G. J. Spencer, 1938); and a fly from Spruce Brook, Newfoundland, on *Hylocichla f. fuscescens*, with 1 female *Brüelia* sp. attached to the side of the abdomen.

11. C. M. Herman (1937) mentioned a fly from North Eastham, Massachusetts, on *Molothrus a. ater*, bearing 2 Mallophaga, one of which was later identified by G. B. Thompson (1947) as a species of *Philopterus*.

12. T. Clay and R. Meinertzhagen (1943) reported a fly from Groton, Massachusetts, on *Turdus m. migratorius*, bearing two female *Philopterus* sp., one attached to each side of the abdomen.

13. A specimen from Forest Hill Borough near Pittsburgh, Pennsylvania, on *Hylocichla mustelina*, carried a louse when it was taken, according to the collector, A. D. Kirk.

14 and 15. At Woodacre, Marin Co., California, J. Maillard

collected the same day on *Zonotrichia coronata*, presumably on one bird, 4 flies, two of which carried lice: a male had 4 *Brüelia* sp. fixed on the dorsum of the abdomen, near the tip; a female had 1 *Brüelia* sp. in the same position.

16 to 29. I have seen the following specimens carrying lice, all collected from living, trapped birds by B. S. Bowdish at Demarest, New Jersey. Male on *Dumetella carolinensis*, with 1 louse near the middle of the hind dorsal margin of the abdomen; a photograph of this specimen, published by MacArthur (1948, p. 386, fig. 233), is reproduced in my Fig. 20. Male on *Turdus m. migratorius*, with 3 lice, 2 on the left and 1 on the right side of the abdomen. Female on *Hylocichla mustelina*, with 2 lice, one on each side, ventrally and close to the sides of the abdomen. Female on *Turdus m. migratorius*, with 2 lice, one on each side of the abdomen. Female on *Turdus m. migratorius*, with 1 louse on the dorsal left side of the abdomen, close to the base. Female on *Melospiza m. melodia*, with 2 lice, one on each side margin, about mid-length of the abdomen. Female on juvenile *Turdus m. migratorius*, with 2 lice on the abdomen, one on the left side near the base, the other on the right side near the apex. Female on *Melospiza m. melodia*, with 2 lice, one on each side margin of the abdomen. Female on *Toxostoma rufum*, with 2 lice on the dorsum of the abdomen, one on the left side at about mid-length, the other on the right side near the apex. Four females on three *Cyanocitta c. cristata*, each with 1 louse on the side of the abdomen. Female on *Cyanocitta c. cristata*, with 2 lice on the abdomen.

30. MacArthur (1948, p. 385) records a male from *Turdus m. migratorius* at Demarest, New Jersey (B. S. Bowdish), with 8 lice "clinging to the rounded lateral abdominal surface, arranged side by side, their heads all directed toward the center of the abdomen."

31 to 34. Mr. K. MacArthur sent me for publication the following additional cases, not seen by myself, based on flies collected also by B. S. Bowdish at Demarest, New Jersey, from living, trapped birds. Male on *Dumetella carolinensis*, with 1 louse on the left side of the abdomen. Male on juvenile *Turdus m. migratorius*, with 7 lice on the abdomen, 3 dorsally, 3 ventrally and 1 on the right side. Female on *Icterus galbula*, with 1 louse on the right side of the abdomen. Female on *Hylocichla f. fuscescens*, with 1 louse on the right side of the abdomen.

35. Female taken by H. A. Drew on *Dryobates v. villosus*, at

Barre, Vermont, carried 1 louse on one side about mid-length on the dorsum of the abdomen.

36 and 37. At Oak Bluffs, Martha's Vineyard, Massachusetts, a female on *Melospiza m. melodia* had 1 louse (*Brüelia* sp.) fixed to the back of the abdomen; another fly on *Spizella pusilla passerina* also carried 1 louse of the same genus.

38. Male taken by A. E. Brower, July 29, 1932, on Mt. Desert Island, Maine, on *Hylocichla guttata faxoni*, had 2 lice, one fixed on each side near the tip of the abdomen.

39. Male taken by S. K. Carnie, October 12, 1950, at Berkeley, California, on *Zonotrichia coronata*, carried a louse on the side of the dorsum of the abdomen close to the basal laterotergite.

40. Female taken by Roy Wing at Euchre Mt., Lincoln Co., Oregon, on *Cathartes aura teter*, June 3, 1948, carried 4 Mallophaga at the tip of the abdomen, 3 on one side, 1 on the other. These lice were identified by Mr. R. L. Edwards as a species of *Brüelia* normally found on some fringillid passerine host. This seems to indicate that the *Ornithomyia* had strayed very recently from some passerine prey caught by the vulture, the latter not being known otherwise as a host of *O. fringillina*. The case is also a definite example of a louse straying onto the wrong type of host following transport by a hippoboscid.

41. Female on *Pipilo fuscus falcifer*, taken at Berkeley, California, August 28, 1949, by H. E. Childs, Jr., carried a louse on each side of the abdomen, one before mid-length, the other close to the tip.

42. Female on *Melospiza m. melodia*, taken at Lake of Two Rivers, Algonquin Park, Ontario, August 20, 1950, by D. M. Davies, carried one louse on the right side edge, near the base of the abdomen.

C. *Ornithomyia remota* Walker (= *O. paricella* Speiser; *O. chilensis* Reed). Although only some 50 flies of this species were seen, 6 of them carried Mallophaga, the proportion being higher than usual for *O. fringillina*.

1. Inaccessible Island, Tristan da Cunha Group: female from *Nesocichla eremita wilkinsi*, collected by Y. Hagen, January 20, 1938, carried two lice fixed to the tip of the abdomen.

2 to 5. Valparaiso, Chile: four specimens, collected and reported by E. P. Reed (1932), carried lice which were determined by Ewing as a species of *Brüelia*. Male on *Diuca d. diuca* (= *Diuca grisea*), with one louse. Female cotype of *O. chilensis*, from an unknown host, with 3 lice, one on the left and 2 on the right side

of the abdomen. Female from an unknown host, with 2 lice, one on each ventral side of the abdomen. Female from an unknown host, with one louse at about mid-length on the right ventral side.

6. Maquehue, Temuco, Chile: female on *Colaptes p. pitius*, collected by R. M. Middleton, with one louse attached near the tip of the abdomen (case published by MacArthur, 1948, p. 385).

D. *Ornithoctona erythrocephala* (Leach). Only 3 cases of phoresy are known thus far for this species, although it is common and widely distributed, with a variety of hosts.

1. A female taken on *Momotus momota chlorolaemus* by W. Weyrauch, at Huacapistana, Río Tarma, Peru, carried one louse.

2. A female taken on *Pionus sordidus saturatus* by M. A. Carriker, Jr., at Cincinnati, Sa. Marta, Colombia, August 29, 1945, carried on the abdomen no less than 15 lice, apparently all of one species; 8 of them (7 adult and 1 immature) were clustered around the apical anal plate; the remainder were fixed to both sides near the base. The lice are a species of *Paragoniocotes* (? *costalimai* Guimarães).

3. A female from Cuba, on *Oreopeleia montana*, bears a louse fixed by the mandibles to a hair, some distance from the integument, at the hind margin of the abdomen.

E. *Ornithoctona fusciventris* (Wiedemann). Only one case known.

1. A female from Boquete, Chiriqui Province, Panama, on *Pseliophorus tibialis*, carried 2 lice attached to the legs.

F. *Stilbometopa ramphastonis* Ferris. Two cases are known thus far.

1. Guimarães (1944) recorded and figured a fly on *Trogonurus aurantius*, from Rio S. José, State of Espirito Santo, Brazil, with 3 specimens of *Brüelia odontopleuron* (Guimarães) fixed to the sides at the apical half of the abdomen.

2. A female taken on an undetermined toucan (*Ramphastos* sp.), at Sto. Tomás, Izabal, Guatemala, carried one biting louse.

G. *Lynchia americana* (Leach). Only one case of phoresy was ever recorded for this common North American fly. H. S. Peters (1935) reported upon a fly of this species from Hartstown, Pennsylvania, on *Casmerodius albus egretta*, carrying 31 immature specimens of *Ardeicola* (reported as *Esthiopterum*) *botauri* (Osborn), a specific louse of certain wading birds. The lice were fixed to the thorax and abdomen, the fly appearing "to be covered with a white powder." This case presents several unusual features. It is noteworthy for the very heavy infestation with lice, all of which were,

moreover, immature. In addition, the fly had strayed onto an abnormal host, this being the only case to my knowledge of *Lynchia americana* having been taken on a wading bird. The fly was determined by me.

H. *Lynchia albipennis* (Say). G. B. Thompson (1936) recorded a specimen of this species (as *L. botaurinorum*), from an unknown host, at Orizaba, Mexico, carrying 5 lice, *Ardeicola botauri* (Osborn). I have also seen this fly.

I. *Pseudolynchia canariensis* (Macquart), the pigeon-fly, sometimes called *Lynchia maura* Bigot, has been reported in the Old World (India) as carrying lice by Helen Adie (1915, p. 679) and Ansari (1947). Ansari's case was particularly interesting, as the fly came from a wild stock of the domestic pigeon, *Columba livia intermedia*. The following American cases refer to flies from domestic pigeons.

1 and 2. Margaret Martin (1934) observed two flies at Houston, Texas, carrying the pigeon louse, *Columbicola columbae* (Linnaeus): in one case with 3 lice (2♀ and 1♂), in the other with one male louse.

3. Hathaway (1943) recorded and figured a fly from Rio de Janeiro, Brazil, carrying 7 specimens of *Columbicola columbae*.

The cases of phoresy of Mallophaga known from the Old World concern the following species of flies: *Ornithomyia avicularia* (Linnaeus), *O. fringillina* Curtis (= *O. lagopodis* Sharp; *O. chloropus* Bergroth), *O. roubaudi* Séguy (probably a synonym of *O. fur* Schiner), *O. perfuga* Speiser, *Crataerina pallida* (Latreille), *Ornithoica pusilla* (Schiner), *Ornithoza metallica* (Schiner), and *Pseudolynchia canariensis* (Macquart). They were summarized by Thompson (1937; 1947), Clay and Meinertzhagen (1943), and Ansari (1947). A few more recent cases were reported by Hopkins (1947) from South Africa, and by Ash (1952, p. 29), Williamson (1950, p. 23), R. Edwards (1951; 1952) and Thompson (1952b, p. 38) from England.

Phoresy of Psocoptera. The following unique observation by Villeneuve (1913), at Rambouillet, France, may be of interest in view of the close relationship of the book-lice, or Psocoptera, to the Mallophaga. "One autumn day I saw *Lipoptena cervi* running in some numbers from a freshly-killed roebuck [*Capreolus capreolus*], brought to me damp and covered with mud. Most of them carried on the ventral side a small lengthened mass which puzzled me greatly. I have since learned from Mr. Speiser, that this mass

was the dead body of a psocid of the genus *Amphigerontia*. I do not know how to interpret this observation."

Phoresy of Thysanoptera. MacArthur (1948, p. 387) reports that a species of thrips was found on the abdomen of a male *Ornithomyia fringillina*, taken on a live *Toxostoma rufum* by Mr. B. S. Bowdish at Demarest, New Jersey. The occurrence was probably a case of accidental transport; although it is known that certain Thysanoptera are predacious, while others have been observed biting Man or animals.

Phoresy of Pseudoscorpions. Séguy (1936, p. 117; 1939, p. DCCXXVI) states briefly that *Crataerina pallida* transports the small pseudoscorpion (*Chelifer*) that lives in the nests of "swallows." As the author kindly informs me, this remark is based on a personal observation presumably made in the region of Fontainebleau, France. Although the pseudoscorpion is no longer available for precise identification, it may have been the species reported, as *Chelifer cancroides* (Linnaeus), by Büttiker (1944, p. 35), who found it in Switzerland in the nest of a swift, *Apus apus*, the usual host of *C. pallida*. Miss Miriam Rothschild informs me (*in litt.*, 1952) that she found *C. cancroides* in many nests of house martins and swallows in England.

III. REPRODUCTION

The peculiar reproduction by integral or *adenotrophic viviparity* (pupiparity), characteristic of the Hippoboscidae, dominates most activities of these flies and accounts for many features of their structure and physiology. Its origin and further evolution are puzzling problems, so far without satisfactory solution.

Keilin (1916) emphasized the fundamental difference between the relatively simple ovoviviparity of many muscoid Diptera and the pupiparity of the Glossinidae, Nycteribiidae, Streblidae and Hippoboscidae. The first type of viviparity calls for no special method of feeding the offspring in the female's uterus, since the larva develops mostly outside her body. As this type is found normally or accidentally in several unrelated groups of insects, also outside the Order Diptera, it was induced presumably by a factor or combination of factors occurring rather frequently in nature. Yet it is by no means clear what this determining incentive may have been at the start; nor is it certain that it was always the same.

Compared with this, the origin of the incubating or adenotrophic type of viviparity of the pupiparous flies is an even more complex problem. It involves intricate adjustments of structure and func-

tion insuring the full development of all larval instars within the uterus, where the larva is fed solely on the secretion of special milk-glands, until it is ready to pupate. As Keilin expresses it: "In order to achieve this, it is not enough to postulate an adaptation of the adult fly, in some way or other; but it is also necessary to consider the specific and correlated adaptation of the newly-hatched larva, which, originally an independent, free organism undergoing its developmental cycle outside the mother's body, must now become adapted to the new and very special conditions of intra-uterine life. The determinism of this mutual adaptation of larva and mother is no less complicated than that of a parasitic larva and its hosts."

I agree with Keilin that no satisfactory explanation has as yet been offered for the origin of the several types of viviparity of the Diptera. Neither Portschinsky's surmise that all viviparous flies were derived from types with coprophagous larvae, nor Roubaud's theory that pupiparity was induced by the combination of a very rich diet, namely blood, and a high temperature activating the general metabolism of the adult, suffice to account for it. Meanwhile, there may be some value in Keilin's suggestion that, in the *Cyclorhapha* at any rate, the larval adaptations required for successful viviparity possibly appeared first among flies with larvae parasitic upon the tissues of insects or vertebrates. But this leaves the question unanswered as to how the correlated adaptive changes of the female reproductive system actually started. Granted that such changes were initiated in the proper direction, their further development into the near-perfect condition now observed in the pupiparous Diptera, would seem to be explained best by Roubaud's theory. In particular, to be successful, integral viviparity requires, at least in free-living flies, a tropical or near-tropical environment, such as is found nowadays in the intertropical zone and such as seemingly prevailed over much of the Earth's surface during late Mesozoic and early Tertiary times.

Sexual Dimorphism. Apart from the external terminalia, there are no striking secondary (C. H. T. Townsend's tertiary) sexual characters in the Hippoboscidae. The sexes are often difficult to distinguish, especially in pinned specimens where the shrivelled abdomen obscures the terminalia. The few differences are mostly in the number, size or shape of the abdominal tergal sclerites; sometimes also in the relative width of the interocular face, although the eyes are always broadly separated in both sexes, even at the postvertex; and occasionally in the chaetotaxy of the

body and of the legs. *Ornithoetona plicata* (v. Olfers), of the Old World, is exceptional in the genus as well as in the family, in that the tip of the fore tibia of the female ends in a broad, rounded plate, which is replaced by a tuft of stiff setae in the male. As Ferris (1929) pointed out, sexual dimorphism is more pronounced in *Ornithoetona* than usual, which is of interest because this genus is the most primitive of the family. In the female, the abdomen bears 5 large, transverse tergal plates, the 5th sometimes partly divided by a median constriction, followed by an apical pair of smaller sclerites. The male has only 4 median plates, followed by the apical pair. In addition, the hind trochanters of the male of most species bear one or more stout, short, spine-like setae, never present in the female.

There is no convincing evidence that any of the few secondary sexual characters of the louse-flies are of special use in copulation or are connected with pre-mating behavior. The slight morphological differentiation of the sexes and the simplified male terminalia may be correlated with permanent ectoparasitism, since both sexes have the same sedentary habits and similar requirements for shelter and food. They meet, therefore, without much difficulty, and sexual behavior is reduced to a minimum. In this connection it may be of interest that the free-living tsetse-flies (Glossinidae), which are also blood-sucking and pupiparous, show a similar dearth of secondary sexual characters, but are nevertheless endowed with an extremely complex male copulatory apparatus.

Sex Ratio. The exact proportion of the sexes in the normally reproducing population of an insect is difficult to determine. The best approach to the problem is to breed out numerous puparia produced under natural conditions, taking into account possible sexual differences in the pupal mortality. The few available data which come near fulfilling these requirements seem to show that in the Hippoboscidae both sexes are produced in about equal numbers. Coatney (1931), in Iowa, found that of 221 *Pseudolynchia canariensis* bred from puparia, 96, or 42.9 per cent, were males and 125, or 57 per cent, females. Schuurmans Stekhoven and his co-workers, in Argentina, obtained for the same species among 269 bred flies, 142, or 52.8 per cent, males and 127, or 47.2 per cent, females (unpublished observations). The slight observed differences in the proportion of the sexes are cancelled out by these two experiments. Schuurmans Stekhoven (1923a, p. 29), in Indonesia, bred 968 flies from puparia of *Hippobosca variegata* (= *H. maculata*), 473, or 48.8 per cent, being males and 495, or 51.2 per cent, females. Herman

(1944, p. 117), in California, also obtained a sex ratio of approximately 1:1 from puparia of *Stilbometopa impressa* reared in the laboratory: in 1941, of 69 bred flies, 39 were females and 30 males; in 1942, of 19 flies, 8 were females and 11 males.

Sex counts of adults collected at random on the hosts sometimes give similar results. Thus Schuurmans Stekhoven (1923a, p. 29), in Indonesia, found both sexes of *Hippobosca variegata* (= *H. maculata*) in about equal numbers on horses: of 1562 caught flies, 804, or 51.4 per cent, were males and 658, or 48.6 per cent, females.

More often, however, females tend to predominate on the hosts, because the males are either actually short-lived or more exposed to accidents. Sometimes males are rare, even in fairly large lots taken from a single host, particularly during the colder months, when reproduction may be slowed down or at a standstill. For instance, only one male was found among 29 deälated *Lipoptena depressa* taken from one black-tailed deer, *Odocoileus hemionus columbianus*, at Tilden Park, Berkeley, California, by Mr. I. B. Tarshis, January 14, 1949 (personal communication). G. J. Spencer (1938, p. 42) noted 51 females and 30 males in a lot of 81 *L. depressa* taken from one black-tailed deer in British Columbia. Hardenberg (1927, p. 13; 1929, p. 509) found 83 females and 46 males in a lot of *L. cervi* collected on deer in the Netherlands.

The true sex ratio of *Melophagus ovinus* does not appear to have been determined by breeding puparia. W. C. Miller (1925), in England, stated that in random counts of adults on sheep females outnumbered males about 2 to 1. Hardenberg (1927; 1929), in the Netherlands, found that 14 different lots taken from sheep contained in all 501 females and 338 males, but that males predominated in some lots and that both sexes were equally represented in one. In three random collections made in Germany by Kemper (1951, p. 236), the females outnumbered the males in 2 cases and the males were more numerous in one; the totals were 135, or 48.7 per cent, females and 142, or 51.3 per cent, males.

Hardenberg (1927; 1929), in the Netherlands, bred 22 males and 20 females of *Stenopteryx hirundinis* from puparia found in nests of the house martin, *Delichon u. urbica*; while of 111 adult flies collected in the same nests 72 were females and only 39 males. Huzimatu (1938) obtained similar results for this species (which he calls *S. nipponica*), on the black-chinned martin, *Delichon urbica dasypus*, in Japan: of 188 adults taken from 12 nests, 106 were females and 88 males.

Kemper (1951, p. 235), in Germany, collected at the nesting

sites of swifts, early in June, 54 female and 23 male *Crataerina pallida*; at the end of July and in early August, 43 females and only 9 males. He concluded that the females outlive the males, but granted that the numbers were too small to warrant definite conclusions.

The sex ratios of the common species of *Ornithoica*, *Ornithomyia*, and *Ornithoetona* have not been determined by breeding. In *Ornithomyia* the females usually outnumber the males on the hosts. Thompson (1940, p. 114) states that, in a series of *O. avicularia* and *O. fringillina* taken in England from 75 trapped live birds of 14 species, from June to September, 61.5 per cent were females and 38.5 per cent males. His table shows that of 89 *O. avicularia* collected, 55 were females and 34 males, and of 36 *O. fringillina*, 28 were females and 8 males. The discrepancy was less pronounced among flies collected from trapped live birds in 1949-1950 by Ash (1952), in Berkshire, England: of 55 *O. avicularia* sexed, 47.3 per cent were males and 52.7 per cent females; of 53 *O. fringillina*, 60.4 per cent were males and 39.6 per cent females. Ash (1951) reported also a preponderance of females in Oeland, southern Sweden: 15 *O. fringillina* taken from 13 species of migrants trapped between August 27 and September 15, 1950, were all females; while only one male was found among 16 *O. avicularia* from 3 species of birds; but the numbers are too small to be significant, owing to the scarcity of flies on migratory birds in that locality, since only 35 of the 1482 trapped birds carried flies. The disproportion of the sexes was slight in a lot of *O. fringillina* collected by Mr. B. S. Bowdish from trapped birds at Demarest, New Jersey, between July 7 and October 29, 1950: of 46 flies taken on 13 species of birds, 28 were females and 18 males; in 1947, of 29 flies taken on 11 species of trapped live birds, between July 29 and August 19, 15 were females and 14 males.

According to Schuurmans Stekhoven and his co-workers (*in litt.*, 1952), at Tucumán, Argentina, of 382 adult *Pseudolynchia canariensis* collected on domestic pigeons, 213, or 55.7 per cent, were males and 169, or 44.3 per cent, females.

A series of 61 *Lynchia americana* from one *Bubo v. virginianus* near Ithaca, New York, consisted of 39 females and 22 males (J. Bequaert, 1945a).

Mr. I. B. Tarshis informs me (*in litt.*, 1952) that during the summer of 1952, in the Bitterwater area, San Benito Co., California, of 283 *Stilbometopa impressa* caught on quail, *Lophortyx californica*, 155, or 54.7 per cent, were females and 128, or 45.3 per cent,

males. Of 135 *Lynchia hirsuta* taken on the same birds, 79, or 58.5 per cent, were females and 56, or 41.5 per cent, males.

Maturation Period. Most adult insects go through a period of sexual maturation, during which in the male the spermatozoa develop so that mating can be effective, while in the female the ova reach a stage at which they can be impregnated. In his experiments with female *Melophagus ovinus*, in Wyoming, Swingle (1913) thought that he was determining the maturation period. Actually he observed the time elapsing between the emergence of a female and the deposition of her first full-grown larva, a combination of the true maturation period of the first ovum in the ovariole and the duration of the larval development in the uterus.

Swingle (1913), in Wyoming, noted that of 29 keds newly emerged on December 1 and 2 and placed at once on a lamb, some were copulating on December 6; from which he concluded that keds could mate when 3 to 4 days old. Later experiments by Graham and Taylor (1941), in Australia, indicated that male sheep-keds require 10 to 11 days to reach sexual maturity; while the female must be 5 to 6 days old before her first ovum can be fertilized; but mating may sometimes be attempted 24 hours after emergence. Therefore, the physical act of mating does not necessarily prove that either the spermatozoa or the ova are fully developed. This conclusion was also reached in England by Evans (1950), who confined newly-emerged males and females in small cages attached to the flanks of sheep, each cage containing two pairs. The males did not attempt to copulate until they were 10 or 11 days old, and in one instance not until the 13th day. Pupating larvae were deposited as a result of these matings 7 to 8 days after copulation. Swingle (1913) had concluded from a long series of experiments that female keds void a first larva from 14 to 30 days after emerging; but his very long pre-larviposition periods did not correspond to the true sexual maturation periods of the ova and they may also have been due in part to the sexual immaturity of some of the males he placed with the females. Evans' (1950) more careful experiments disclosed that, if a newly-emerged female placed with a fully-mature male (not a newly-emerged male) copulates within 16 hours or less, she does not larviposit until 12 to 14 days after mating (13 days on the average). He found that, once a first larva has been voided, the minimum gestation period of each of the succeeding larvae is 7 to 8 days (6 to 7 days, according to Graham and Taylor, 1941); a newly-emerged female therefore requires from 5 to 7 days to mature a first ovum so that it can be impregnated.

Doubtless similar conditions prevail in other Hippoboscidae, but little attention has been paid thus far to this topic. According to Adie (1915, p. 672), *Pseudolynchia canariensis* bred in captivity will feed on a pigeon within a few hours after emerging and the female voids a first larva when 7 to 8 days old. Prouty and Coatney (1934) noted for the same species that, if the sexes were separated after they emerged and put together after 12, 36 and 72 hours, copulation never took place until the third day and then only if the male had not recently fed. Hare (1945b) states for *Lipoptena depressa*: "Blood sucking begins the first day after host contact The sexually mature stage of the imago is reached after about 12 days of feeding, and marked post-imaginal growth of the abdomen. After copulation, the first larva is deposited by the female on the 16th to 19th day. Subsequent larvae are produced singly, at three-day intervals." This would seem to imply an unusually protracted maturation period; unfortunately the detailed observations on which Hare's conclusions were based have not been published. Theodor (1928, p. 288) states that the female of *Lipoptena capreoli* (= *L. caprina*), in Palestine, is about 3 weeks old when she deposits her first larva.

In view of the very few larvae produced by a single hippoboscid female during her lifetime, the non-productive period in early adult life should not be overlooked in attempts to compute the rate of reproduction.

Mating. There is at present no evidence of parthenogenesis in the Hippoboscidae, mating being essential for reproduction. Graham and Taylor (1941) and Evans (1950) showed this experimentally for *Melophagus ovinus*. Evans kept newly-emerged, unmated females on sheep for 28 to 30 days without obtaining puparia; but the same flies started producing larvae a few days after males were placed with them. The female ked stores in her genital tract at one mating sufficient sperm to impregnate some 13 eggs in succession during her lifetime of approximately 4 months, as Graham and Taylor (1941) observed in one experiment. Nevertheless, repeated matings of the same female usually occur when male keds are present. *M. ovinus* mates on the host. The procedure was first observed by Dufour (1845, p. 82): the male climbs onto the female's back, clasps his legs tightly around her sides, then backs up, so that the tip of his abdomen reaches beyond that of the female, and, curving the tip upward, inserts the penis and penis valves in the vulvar opening. The duration of a mating varies and Evans (1950) observed that it lasted 24 hours in one case.

Roberts (1927, p. 18), in Wales, England, observed the mating of *Hippobosca equina* in the pelt of cattle, in nature, and described it as follows: "The claspers [penis valves] are remarkably adapted to facilitate coitus without undue flexure on either member, the non-elasticity and absence of segmentation of which are a great hindrance to successful copulation by ordinary methods. The male anal extremity has a deep invagination, whereas in the female the anal extremity and genitalia protrude—the complex being termed the hypopygium. Thus, during copulation, the hypopygium of the female is grasped by the claspers of the male and held in position in the invagination. The limited flexibility of the insects due to dense chitination of the integument and absence of segmentation makes some such arrangement necessary. As the claspers hold the flexible hypopygium this obviates undue stress on the enclosed organs, also shortening and unifying the passage effected between the male and female genital tubes—that is, the end of the penis is much nearer the receptaculum seminis. In *H. equina*, during copulation, the female remains in her original position as when feeding, thus giving the male a vertical pose. No courtship preliminaries were observed, and the psychological moment of acquiescence on the part of the female still remains a mystery." Schuurmans Stekhoven (1923), in Indonesia, saw *Hippobosca variegata* (= *H. maculata*) copulate on horses, although a pair did mate also in a cage away from a host. The male may repeat the performance even the same day with the same female. During copulation the male sits on the back of the female, which holds the wings fully spread out, and he grasps her neck with the fore legs; his abdomen bends under that of the female and the two remain united, as a rule for several minutes.

In *Lipoptena* mating is usually observed on the host; although Cowan (1943), in British Columbia, saw on one occasion in late September two winged *L. depressa* copulate in flight, the united pair landing on his clothing. Hartmann (quoted by Stein, 1877), in Germany, found many mated pairs of deälated *L. cervi* on deer throughout the winter, the male sitting on top of the female. If a pair is kept in a vial, the female may sometimes void a larva, this being invariably followed by a new mating. A mated pair of *L. depressa* was found on a white-tailed deer, *Odocoileus virginianus leucurus*, early in January in Idaho by Mr. Turner (J. Bequaert, 1942a, p. 124); both individuals were deälated and old, having doubtless emerged several weeks before. The male sat on top of the female's abdomen, his palpi reaching her scutellum; his apical

tergites were curved under the anal end of the female and the three rod-like pieces of the aedeagus inserted in the vulvar opening. The pair were so firmly united that a cleared slide could be made showing them *in copula*. It is noteworthy that mating occurred in nature on the host in mid-winter, as Hartmann had observed for *L. cervi*. Cowan (1943) noted that in *L. depressa* copulation is often repeated on the host and that it is unusual to find a gravid female without a male clinging to her abdomen, so that mating takes place immediately following the expulsion of a larva. Of 56 keds taken from one deer on January 6, 46 were copulating and one female containing a black larva was also attended by a male. Theodor (1928, p. 287), in Palestine, witnessed the mating of *L. capreoli* (= *L. caprina*) on the domestic goat. Dr. L. R. Guimarães recently sent me a pair of *L. mazamae* found mated on a brocket, *Mazama americana*, in Brazil.

Coatney (1931) wrote of *Pseudolynchia canariensis*, the pigeon-fly: "Mating generally begins while the flies are on the host. The female spreads her wings widely, then the male holds on to her neck with his fore legs and bends his abdomen ventrally to insert the penis. The male makes rhythmical movements with the abdomen while *in copula*. The flies usually leave the birds during copulation and retire to some darkened corner or crack, where the female deposits her offspring, although I have observed single females deposit larvae." Prouty and Coatney (1934) later added some interesting details: "The male mounts the female from the side with a swift running motion. His fore legs are clasped around the female just posterior to the head, and the hooks on his tarsi are sunk into the fleshy triangle formed by the female's two front legs and the ventral chitinous plate. The second pair of legs clasp the female at the junction of the thorax and abdomen. Her wings are separated widely by his third pair of legs, which are then projected posteriorly. The entire process of mounting and separating the wings is so swift as to prohibit observing the exact sequence of events, but it is thought to be almost simultaneous. The abdomen of the male is now strongly flexed ventrally and closely applied to the body of the female, to allow the insertion of the intromittent organ. During copulation the female is sometimes seen to stroke the abdomen of the male with the third pair of legs. The pair remain united for a variable time, anywhere from a few minutes to 2 hours, when the male suddenly dismounts. When the female takes the initiative in severing contact she will be seen to jerk from side to side. If this fails, she raises herself on her first and second

pair of legs, and dislodges the male by pushing on his abdomen with her third pair of legs." According to recent observations (now in press) by Schuurmans Stekhoven and his co-workers, in Argentina, mated pairs of *P. canariensis* are often found on adult pigeons, as well as on squabs in the nests.

M. Leclercq (1946, p. 145) observed a pair of *Crataerina pallida* mated on a swift, *Apus apus*, at Angleur, Belgium, in May.

Huzimatu (1938, p. 61), in Japan, states that *Stenopteryx hirundinis* (= *S. nipponica*) usually mates while the flies are still in the nest of the black-chinned martin, *Delichon urbica dasypus*, presumably shortly after emerging and before they reach a bird. The male holds the neck of the female with his fore legs and bends his abdomen ventrally to insert the penis. He moves his abdomen rhythmically during the act of copulation.

O'Mahony (1950b) records pairs of *Ornithomyia fringillina* taken in *copula* on birds in Ireland.

There is no evidence in the Hippoboscidae that repeated mating is ever injurious to the female or causes accidental death. In the bird-flies particularly, pairing of the same female is rarely frequent enough.

Whether or not the sexes are mutually attractive and by what means is not known. They might possibly meet by chance as they swarm or move through the pelt or plumage, in the nests or over the breeding grounds of the hosts. There appears to be little if any preliminary courting or other form of pre-mating behavior; although Hase (1927, p. 193) believes that copulation might be preceded by certain peculiar so-called "play flights," which *Hippobosca equina* indulges in at times, flying off and on the host.

Intra-Uterine Development. The impregnation of the egg after it reaches the uterus, the embryological growth in the egg, the hatching of the first larval instar and the growth of the three successive larval instars, separated by two moults, all proceed within the abdomen of the female, hence escape direct observation. It is impossible to determine how long each of these stages lasts; but the total duration of the intra-uterine development may be determined by timing the successive larvipositions of normally fed females, after the first larva has been voided. The first-born larva cannot be used for the purpose, since, as shown above, the newly-emerged female goes through a maturation period of several days before the first egg is impregnated.

In *Melophagus ovinus*, Evans (1950, p. 460) observed for six individual cases, in which a female was placed, immediately after

voiding her first larva, with a mature male in a cage attached to a sheep, that the second larva was deposited 7 to 8 days (7.3 days on the average) after the first, and the third about the same length of time after the second (7.5 days on the average). Graham and Taylor (1941), in Australia, had previously determined that the larvae were voided at intervals of 6 to 7 days.

Larviposition. Long before the Europeans, the Chinese evidently were acquainted with the peculiar reproductive behavior of the Hippoboscidae, having observed it for *Hippobosca longipennis*, which often swarms on dogs in the Far East. It is recorded in the "*Chien Wu*," by Li Su (dated approximately 1582 A. D.), that "dog-flies deposit among the hairs of the dog their nits [puparia], which after molting become flies." In the Western World, the first similar observation appears to be that of Frisch (1736, p. 40), in Germany, for the sheep-ked, *Melophagus ovinus*. He noted in his account of the "Schaaf-Laas" that it deposits one "egg" at a time, as large as the ked's body, which "egg" is stuck to the wool, and that inside it the "louse" develops "as in an aurelia" or chrysalis. He figured both the adult and the so-called "egg" (Fig. XVIII, No. 2), the latter being the earliest figure of a hippoboscid puparium on record.

The great French naturalist, Réaumur (1742), however, was the first to interpret correctly the peculiar larviposition of the louse-flies. He described the process accurately for *Hippobosca equina*, in the following passage, translated from the French: "It must be a great performance for a fly to release from her body an egg exceeding in size that of the body itself. However, she deposits this over-sized egg with as much ease as other flies lay theirs of a size better proportioned to their own. It all happens in an instant; at any rate I saw a moment later the whole egg of which I had just seen the tip appear from the hind part of the fly. Everything that Nature wants animals to do, is made easy for them. Beneath the anus of the fly there is an opening normally covered with a triangular, sclerotized plate. This opening expands to the extent needed for a not too laborious parturition. Perhaps it is to provide for the expansion of this opening and to keep its margins from being torn in spite of the great stretching, that the hind part of the body is broader than the remainder. The fly just delivered of such a large egg does not seem to be particularly exhausted; it runs and flies off at once as usual. I have nevertheless witnessed some laborious parturitions and I was not sorry that they were difficult. A fly which had been squeezed too much by the fingers that had caught

it, sometimes started voiding between my fingers an egg as yet immature. The operation was then protracted, so that I had more time to observe the gradual excessive dilatation of the opening through which the egg must pass. The narrowest end, bearing a large black spot, is seen first. This spot comes out first; once it is in full view, a white-colored portion soon makes its appearance; next the whole egg is pushed out of the body." Réaumur not only saw the female fly void the larva, but he also witnessed how it first turns chestnut-brown and later black, to form a hardened object from which he bred a new fly exactly like the mother. Furthermore, upon dissecting one of the developing puparia, he found that it produces a true pupa or "nymph" inside the hardened case. Although he uses the word "egg," he recognized correctly that the female voids a full-grown larva or potential pupa, and not a true egg, and he realized fully the significance of his discovery. He also found in swallows' nests similar black puparia from which he bred the "spider-fly" he had described some years before (1738), a species now called *Stenopteryx hirundinis*. Réaumur's observations on *Hippobosca equina* were later confirmed by Bonnet (1762; 1764; 1775; 1779; 1782; 1786) and Degeer (1772).

The actual process of voiding the mature larva is much the same for all Hippoboscidae. The type of environment selected for larviposition is of greater interest than the performance itself. The following summary shows that most species void the larva away from the host, in a fairly safe place chosen for the express purpose by the gravid female. Larviposition on the host is known to occur normally in the mammal-infesting Melophaginae only. Pertinent observations for the Alloboscinae of lemurs and the Ortholfersiinae of wallabies are as yet lacking.

In the Melophaginae, the freshly voided larva of *Melophagus* leaves the vulva covered with a glue-like secretion, which, though readily soluble in water, hardens upon drying and sticks the puparium to the hairs of the host. On sheep, the puparia of *M. ovinus* are usually found attached half an inch to an inch from the skin, where the flies emerge. Graham and Taylor (1941), in Australia, observed that the distance from the skin tends to increase with the length of the wool. They also found that larviposition generally occurs on the lower part of the sheep's body, 45 per cent of the puparia being placed on the under side of the neck. These observations were confirmed and extended by Evans (1950, pp. 472-473), in England, who points out that the viability of the

puparia is strongly influenced by the temperature, which interferes with the normal pupation when too high.

In *Neolipoptena*, *Lipoptena*, and *Echestypus*, which drop the wings after reaching the host, the gravid female must also larviposit in the pelt; but the puparia, being smooth, dry and not fastened to the hairs, eventually drop off and are scattered at random on the ground. To be true, Hardenberg (1927, p. 4; 1929, p. 499) includes *Lipoptena* among the Hippoboscidae that leave the host in order to larviposit "somewhere in the vicinity in cracks of the soil, of tree bark, etc."; and Hase (1939b, p. 411, footnote) seems to imply that Hardenberg had actually found puparia of *Lipoptena cervi* in such locations. I can find no evidence in Hardenberg's papers that he ever found a puparium of a deer-ked in nature or that he saw a female *Lipoptena* leave the host in order to void a larva. Cowan (1943, p. 183) concluded from his protracted study of the reproductive behavior of *Lipoptena depressa* on black-tailed deer, *Odocoileus hemionus columbianus*, in British Columbia, that it larviposits on the host and that the puparia later drop out of the pelt. Hare (1945b) definitely states that he found puparia of *L. depressa* in the wild among surface débris of the forest floor, but gives no further details. It is to be expected that puparia of *Lipoptena* will be found occasionally in the host's pelt, shortly after larviposition, particularly if the hairs are very long and dense or when the larvae are voided on the motionless body of a dead host. Thus v. Siebold (1845), in Germany, found puparia of *L. cervi* on a European elk, *Alces alces*. Darling (1937) saw some puparia amidst the hair of a red deer, *Cervus elaphus*, in Scotland, after March, but noted their absence during the winter. There are a few other similar records for the European deer-ked. Dr. W. L. Jellison sent me puparia of *Neolipoptena ferrisi*, which he found loose in the heavy winter haircoat of a white-tailed deer, *Odocoileus virginianus leucurus*, in Montana, during February. All these findings do not prove, however, that the puparia normally remain in the pelt during pupation or that new keds emerge regularly on the host in nature. Theodor (1928, p. 288) and Aschner (1931, p. 370), in Palestine, noted that the puparia of *Lipoptena capreoli* (= *L. caprina*) are deposited on the goats, but do not remain there. They drop off and are difficult to find where goats rest in the open, but may be obtained by keeping an infested goat in a small stable with a hard floor, which can be searched every morning. The puparia of *Lipoptena* are difficult to locate in nature after they drop from wild animals. Nevertheless, in Germany, Ratzeburg (1869, *Die*

Waldverderber und ihre Feinde, 6th Edition, p. 423) reported that Ulrich found in November numerous black, shiny puparia of *Lipoptena cervi*, looking like peony-seeds, strewn over the snow where European elk, *Alces alces*, had been resting.

Probably all species of *Hippobosca* larviposit away from the host in appropriate spots selected for the purpose. Roberts (1925, p. 88) observed the process in England for *H. equina*, in the open under natural conditions: "When the larva is mature the females leave the host, but it is a matter of great difficulty to observe the act of deposition, which takes place among the organic débris that collects at the base of the stems of bracken (*Pteris aquilina*). After leaving the host the females settle on a frond of bracken and, dropping to earth, choose a situation in the decaying humus where the larva is deposited. The writer has observed this on five separate occasions all during early August. The larva is partially buried in the humus as soon as extruded. It is of a globular shape and creamy white in color at extrusion, with a black cap and two conical projections at that pole. It is incapable of any individual movement and has little or no trace of segmentation. It pupates after the passing of a few hours, the larval integument simply becoming chitinised to form the pupal casing, whilst a gradual darkening of the integument takes place until the puparium is black. It is not essential for the larva to be placed in suitable surroundings for pupation as this will take place, in many instances, in a glass tube or other receptacle. In addition to the five cases of actual larva deposition in decaying humus noted above, the writer discovered twelve pupae among organic débris beneath the bracken. Further, two pupae have been discovered on pasture land (not far from bracken) lying in crevices of twisted roots of grass. It is believed that this is an unusual occurrence. The nature of the decaying humus beneath the bracken lends support to the assumption that this is the normal habitat of the pupae, as nearly all observed have been found here, and the actual deposition of larvae has been observed to occur here. In this position, there is shelter from heavy rains, while moisture drips down from the fronds. The sun does not penetrate strongly, and a continuous moisture is assured. The decay of the humus possibly supplies a certain amount of warmth during decomposition." Patton and Cragg (1913) found puparia of *H. variegata* (= *H. maculata*) in calfsheds in India. Fletcher (1920, p. 101) mentions that P. G. Patel found 5 puparia of this fly in the nest of a mynah, *Acridotheres tristis*, at Pusa, India. Schuurmans Stekhoven (1923, pp. 21 and 47-71),

in Indonesia, also carefully observed the larviposition and puparia of *H. variegata*, particularly on Soemba, where the fly is very abundant on horses and cattle. He saw a gravid female leave a horse, fly about for a few seconds and then choose a crack in which puparia had been found previously. After a brief preliminary inspection, the fly held the tip of the abdomen over the crack in which it dropped a larva in about three seconds. The larva seemed to be moist or even slightly sticky upon being voided, as it dangled sometimes for a while from the tip of the abdomen before dropping. Larviposition occurred in the daytime between 10 A. M. and 5 P. M., but mostly in the afternoon. Where infested horses were kept overnight in an open-shed stable, puparia could be collected particularly in feeding troughs and in corners of the pillars and beams of the roof. However, the number found indoors was so small in proportion to the heavy fly infestation, that larviposition evidently occurred mostly outdoors during the day. This was confirmed by further investigation. Puparia were more difficult to find in the open, because of the wide area involved, even though certain special locations are selected for larviposition by the females after leaving the host. A few were found on the ground in shaded places, but this seemed to be an exceptional location. The majority were placed some distance above the ground in well-sheltered spots, such as crevices or holes in fences or cavities of the trunks of coconut palms and trees. Sometimes cracks in the bark of trees were almost filled with developing and emerged puparia. Evans (1895, p. 79) quotes one "J. B. D." as having found a puparium of *H. longipennis* (= *H. canina*) in the long hair of a dog's neck in India, possibly an unusual occurrence. Patton (in Patton and Evans, 1929, p. 404), in India, saw a female *H. longipennis* (= *H. francilloni*) leave a dog, fly onto a wall, and, after running over it, swiftly disappear in a crack. The fly remained there a few minutes and was caught as it reappeared. A larva was found a short distance within the crack. Austen (1909, p. 171) reports that 2 puparia of *H. camelina* were found by A. E. Eaton at Biskra, Algerian Sahara, by digging at the roots of an *Euphorbia*, a fly emerging from one of them later; he concludes that the puparia had been deposited by females which had crawled intentionally into cracks for the purpose. It would be of special interest to know where the puparia of *H. struthionis* are placed. When publishing Janson's original description of this species, Ormerod (1889) noted that "pupal cases" were received with the adults; but they may have been from larvae

newly voided by captured gravid females and it remains doubtful that puparia actually occur in the plumage of living ostriches.

Johnson (1929, p. 52) reports puparia and adults of *Ornithoica vicina* (cited as *O. confluenta*) in the feathers and some puparia also in the ears of a great horned owl, *Bubo virginianus*, in Massachusetts in late September. If puparia are voided and remain regularly in the feathers of owls, this may be due to the unusually dense and thick plumage of such birds; it may perhaps not occur for the same species of fly when it lives on the small passerine birds which are also its common hosts. At Rensselaerville, New York, in September, 1951, Dr. K. C. Cooper caught a newly-emerged *O. vicina* on a window pane in a barn-room where a phoebe, *Sayornis phoebe*, had been nesting; possibly it came from a puparium in the abandoned nest of this bird. The larviposition of *Ornithoica* should be investigated more carefully.

Among the Ornithomyiinae information is most complete for *Crataerina pallida*, the closely allied *C. melbae*, and *Stenepteryx hirundinis*, the common subapterous parasites of Old World swallows, martins and swifts. Their smooth puparia are often numerous in the nests of the hosts during the birds' breeding season, and later during fall and winter in abandoned nests, where the flies hibernate in the pupal stage. Réaumur (1742, p. 576), in France, first saw in swallows' nests black, shiny "grains" [puparia], from which he bred flies exactly like those he had figured some years before (1738, Pl. 11, figs. 1-5) as the "spider-flies of swallows' nests." These earlier figures show clearly that he was dealing with *Stenepteryx hirundinis*, the usual parasite of the house martin, *Delichon urbica*. However, in some observations by later authors, puparia referred to *S. hirundinis* may have been confused with those of *C. pallida*. Modeer (1785, p. 37) mentioned finding them in swallows' nests in Sweden. In Germany, Stein (1849) reported puparia from nests of the barn swallow, *Hirundo rustica*, on which host *S. hirundinis* is perhaps more frequent than has been generally believed, as adults have been found even on nestlings (Britten, 1936). Rossi (1860), also in Germany, found 50 to 60 puparia in an old nest of a house martin, *Delichon urbica*, flies emerging the next May. v. Frauenfeld (1861), in Austria, observed adult flies feeding on nestling house martins; the flies left the birds frequently and one gravid female was actually seen leaving a nestling in order to deposit a larva in the nest; one abandoned martin's nest yielded 22 live puparia in December. F. Löw (1861) also bred this species from a puparium found in a martin's nest in Austria.

Cornelius (1869) reported up to 100 puparia from one nest in Germany; while Sickmann (1885) took from 10 nests at Osnabrück, Germany, 13 empty and 232 live puparia, the latter producing 200 flies the next spring. Speiser (1900) and Bau (1929) likewise bred *S. hirundinis* from puparia overwintering in martins' nests in Germany. In France, Perris (1869) reported finding puparia of *S. hirundinis* in swallows' nests, and H. du Buysson (1923) definitely recorded puparia from nests of *Delichon urbica* in the Department of Allier. In England, Mellor (1919, p. 65) found in martins' nests, in October, puparia from which *S. hirundinis* emerged next May; Evans (1921) found 2 puparia in the lining of a martin's nest; Thompson (1935a) reported 19, 42 and 8 puparia respectively from 3 house martins' nests early in September. Woodroffe and Southgate (1951b, p. 58), also in England, collected in January from a sparrow's nest in a building 3 puparia from which *S. hirundinis* were reared; Mr. G. E. Woodroffe (*in litt.*, 1952) informs me that there were no martin nests in the immediate vicinity, but there were several old ones not very far away; he attributes the record to the common habit of sparrows of roosting during autumn and winter in old martin nests. Mr. Woodroffe also sent me a summary of his findings in some 40 house martin nests which he and Mr. Southgate examined in southern England from September, 1950, to January, 1951, the details to be published shortly by Mr. G. B. Thompson; puparia of *S. hirundinis* were present in nearly all the nests, sometimes in abundance; adult flies were also found during September, but not later. In Ireland, O'Mahony (1944) bred 49 flies from a single martin's nest in the spring and noted that old empty puparia often occurred in the deeper mud layers of which the nest is built, while recent, live ones were more in the looser inner lining. In Japan, Huzimatu (1938) took 209 puparia of *S. hirundinis* (= *S. nipponica*) from 12 martins' nests, from 7 to 47 being found in a single nest.

In Germany, puparia of *Crataerina pallida* were taken in nests of swifts, *Apus apus*, during late fall and winter by Cornelius (1869), who bred flies from them the following April, and by Bau (1929); Kemper (1951, pp. 227-229) reported finding adult flies, as well as living and empty puparia scattered over the floor at the nesting and roosting sites of swifts in holes and corners of buildings in Berlin. In Switzerland, Schneider-Orelli (1937) and Büttiker (1944) observed the breeding of *Crataerina*. Schneider-Orelli found puparia of *C. pallida* and *C. melbae* in November in nests of alpine swifts, *Apus melba*, adults being reared of both species; each

nest contained from 6 to 80 puparia, 53 on the average; only those of *C. pallida* were present in nests of chimney swifts, *Apus apus*. Büttiker (1944, p. 28) states definitely that he saw gravid females of *C. pallida* leave swifts in order to larviposit in the nesting material, returning afterward to the birds. In England, Cutcliffe (1951) noticed many puparia of *C. pallida* in and near the nests of swifts, *Apus apus*, at Ilfracombe, Devon. According to Mr. G. E. Woodroffe (*in litt.*, 1952), puparia of *C. pallida* were found in very large numbers in a colony of nesting swifts in London, in January, 1951.

Ornithomyia biloba usually parasitizes barn swallows, *Hirundo rustica*, in continental Europe, but is often mistaken for either *O. avicularia* or *O. fringillina*. This fly also larviposits in the host's nest. F. Löw (1861) reported 150 live and 1150 empty puparia (as *avicularia*) from the several layers of an old barn swallow's nest at Vienna, Austria; some of the empty puparia might have accumulated from previous years, as swallows often use old nests again. In France, Perris (1869) mentioned puparia of this fly (as *O. avicularia*) from swallows' nests, while H. du Buysson (1923) reported them (as *O. fringillina* or *tenella*) from nests of *Hirundo rustica* in the Department of Allier. In Germany, Stadler (1948) stated that empty and live puparia of what he calls "*Ornithomyia fringillarum*" occurred in a nest burrow of sand martins, *Riparia riparia*, after the birds had left the site in the fall; no doubt he was dealing with *O. biloba*, which is reported also from the sand martin by Eichler (in Niethammer, 1937, 1, p. 458). Cornelius (1869), at Eberfeld, Germany, Sickmann (1885), at Wellingholthausen, Austria, and Sack (1899), at Offenbach a/M., Germany, all found puparia of *O. biloba* (cited as either *O. avicularia* or *O. tenella*) in deserted nests of *Hirundo rustica* during the winter. Sickmann reported 141 empty and 103 live puparia from one nest and bred 95 flies the next spring from this lot. In spite of this evidence, he refused to admit that this fly hibernates as puparia, but held to the belief that the adults either overwinter hidden in cracks or travel to Africa and return from there on the migrating swallows; there is no factual evidence in support of his view.

Information now available shows that the common *Ornithomyia avicularia* and *O. fringillina* also larviposit away from the host. In Germany, Dorn (1913) found in a hawk's, *Accipiter nisus*, nest in July, 5 puparia from which flies called *O. avicularia* were bred the following April to June; the same fly emerged also from puparia collected in a chicken coop and from one found lying on moss in

a forest. In England, Austen (1932, p. 213) figured puparia, presumably of *O. avicularia*, from a tit's nest (*Parus* sp.); both Saunt (1933) and Blair (1949) reported puparia, supposedly of *O. avicularia*, from nesting boxes or nests used the summer before by green woodpeckers, *Picus viridis pluvius*, and possibly afterward by starlings, *Sturnus vulgaris*. Thompson (1938a) added three more instances of puparia in nests of British birds: some of *O. avicularia* were found in nests of a song-thrush, *Turdus e. ericetorum*, and of an owl; others, most probably of *O. fringillina*, came from the nest of a blue tit, *Parus caeruleus obscurus*. Crichton and Campbell (1949) believe that *O. fringillina* overwinters in the nests as puparia, as they found 3 puparia of this fly on December 24 in the nest of a garden warbler, *Sylvia borin*; they suggest also that puparia may sometimes be voided at random in the undergrowth and that this must be the ultimate resting place of those left in nests which fall apart during the winter. Ash (1952) reports from Berkshire, England, 2 puparia in a nest of a song-thrush, *Turdus e. ericetorum*, on July 1st, when the young had just flown; adult flies had been taken previously from the brood in this nest. He notes that he never found puparia of either *O. avicularia* or *O. fringillina* on 80 live juvenile and adult birds of 11 species which were infested with the flies. Mr. G. E. Woodroffe, in England, informs me (*in litt.*, 1952) that he found one puparium of *O. fringillina* in a robin's, *Erithacus rubecula*, nest, in October, and another in that of a house sparrow, *Passer domesticus*, in November. I have seen from the Netherlands an *O. fringillina* bred in June from a puparium found February 27 "in rotten wood of an old willow in a poultry-yard," near Baexum, Limburg, by F. Rüschkamp; also one *avicularia* bred from a puparium found in the nest of a blackbird, *Turdus merula*, near Leiden. In Belgium, Leleup (1937, pp. 316 and 323; see also Collart, 1947, p. 211) collected puparia of *O. avicularia* in March and April from tree holes in which a little owl, *Athene noctua vidalii* (3 puparia), and a wild pigeon, *Columba o. oenas* (5 puparia), had been nesting; some adults were bred the same spring from each lot, so that the specific identification may be trusted. Johnsen (1948), in Denmark, obtained puparia of *O. avicularia* from the nest of a European buzzard, *Buteo b. buteo*, in October, adult flies emerging the next year from March to August; he also found some puparia of this fly in July and believes that the species overwinters as puparia in birds' nests. Shipley (1913, p. 15) states that the puparia of the grouse-fly, *O. fringillina* (= *O. lagopodis*), are usually found in

the nest of the red grouse, *Lagopus scoticus*, in England; he surmises that they remain there over winter for nearly three-fourths of the year, the adults emerging only next June. There is as yet no information on the whereabouts of the puparia of *O. fringillina* in nature in North America, where no hippoboscid puparia have been found thus far in birds' nests, although the insect fauna of nests has been investigated repeatedly.

The following few definite reports of puparia of *Ornithomyia* occurring on birds in the plumage may have resulted from accidental or premature parturitions. O'Mahony (1950) mentions a puparium of *O. fringillina* from the feathers of an unidentified bird (either a wheatear or a meadow pipit) on Fair Isle, Scotland. Eichler (1939b, p. 224) states that a puparium, presumably of *Ornithomyia* sp., occurred in the feathers of a migrating pipit (*Anthus* sp., possibly *A. pratensis*), on Heligoland, Germany.

Herman (1944), in California, described the larviposition of *Stilbometopa impressa*, a parasite of California quail, *Lophortyx californica*, as observed in the laboratory. No puparia were ever retrieved in nature. When about to larviposit, the gravid female stands on the first two pairs of legs. While the abdomen is stroked backward with the hind legs, one on the dorsal and the other on the ventral side, the larva slowly emerges from the vaginal opening, the entire operation taking over two minutes. However, gravid females removed from quail often seem to larviposit instantaneously. According to unpublished observations by Mr. I. B. Tarshis (*in litt.*, 1951), gravid females of *S. impressa* normally also leave the host and eventually drop the prepuparium in some shaded or sheltered spot; but the preliminary stages of larviposition occur while the fly remains on the bird; about two-thirds of the larva protrude from the vulvar opening and the integument has already become harder and amber-colored before the female leaves the host.

Pseudolynchia canariensis larviposits away from the host, according to observations by Adie (1915), Drake and Jones (1930), Aschner (1931, p. 371), Coatney (1931), Prouty and Coatney (1934), and Schuurmans Stekhoven and his co-workers (unpublished). When flies are kept on pigeons in captivity, most puparia are found, not in the actual nesting material where they would be expected to drop if deposited on the birds, but in dry, darkened corners or underneath trays or other objects where the gravid female can hide while voiding the larva. In experiments they may be collected in muslin bags attached below cages with a wire-net

bottom. Coatney actually witnessed larvae being laid away from the host, usually between 7 and 11 A. M.

In all species of *Olfersia* the puparium is densely covered with stiff hairs, with either straight or hooked tips; which might raise the suspicion that larviposition occurs on the host and that the puparia stick to the feathers like burrs. This seems to be erroneous, however, since no such puparia have ever been found on any of the bird hosts. On the contrary, there is some evidence that the gravid females leave the birds; so that the spinose covering probably serves to protect the puparium, either against mechanical injury or by hiding it with adhering debris, or in some other way. Dr. L. B. Lewis (*in litt.*, 1950), who observed *Olfersia spinifera* in bird rookeries on the Pedro Cays, near Jamaica, collected a nest of a frigate bird, *Fregata magnificens*, which contained many puparia of this fly hidden underneath the platform of lime and attached to the twigs of the nesting material.

Little is known of the larviposition of *Lynchia*, although some species of this genus are among the most common louse-flies. According to Schiner (1864, 2, p. 647), Frauenfeld found a puparium of *L. albipennis* (= *L. ardeae*) in a nest of the bittern, *Botaurus stellaris*, in Austria. Champlain (1947) states that *L. americana* occurs frequently on great horned owls, *Bubo virginianus*, in Pennsylvania, throughout the winter, from November until March, when puparia as well as adults may be found in the plumage. The retention of the puparia in the feathers of owls, if actually a normal occurrence, may explain why these birds are often heavily infested, as many as 61 flies having been taken off a single owl. Since *L. americana* is common during the summer on a variety of other birds, such as grouse and diurnal birds of prey, owls possibly act chiefly as winter hosts, from which the species presumably spreads to the other hosts in the spring. A similar explanation possibly applies also to *Ornithoica vicina*, whose puparia have been found likewise on owls during the winter, as mentioned above. Mr. I. B. Tarshis (*in litt.*, 1951) reached the conclusion that the gravid females of *Lynchia hirsuta*, a parasite of California quail, *Lophortyx californica*, leave the host for larviposition, since he found puparia in somewhat secluded tray corners of cages in which he kept infested birds.

Observations on the larviposition are in many cases fragmentary and, moreover, available only for relatively few species, so that one must be cautious about drawing general conclusions. From present evidence, the two species of *Melophagus* appear to be the only louse-

flies whose puparia are deposited and definitely remain on the host until emergence. In most other genera studied for the purpose, either the gravid females normally leave the host for larviposition or the puparia laid on the host eventually drop out of the pelt or plumage. If a few puparia are occasionally found in birds' feathers, it does not necessarily mean that pupal development occurs normally there. It follows from these considerations that the breeding association between the Hippoboscidae and their hosts is rather loose, since in most species the adults emerge away from the host. This peculiarity of their life history is no doubt largely responsible for the low degree of specificity so prevalent among the Hippoboscidae.

Formation of Puparium. Although the normal mature larva of most Hippoboscidae is mostly soft and pale-colored when newly voided, except for the stiff, blackish distal respiratory lobes, it is nevertheless unable to burrow in or to move from where it was dropped; at most it shows sometimes slight contractions and expansions of the anterior or buccal end. It takes definitely no food of any kind once it leaves the mother's body. If parturition is normal, the remainder of the integument of the larva hardens and darkens rapidly, while retaining all the structural features of the larval skin. The larva thus transforms into a typical puparium, as in all Cyclorrhapha.

The process is much the same for all louse-flies. Herman (1944) describes it as follows for *Stilbometopa impressa*: "The larvae, when deposited, are white or cream-colored, although in many cases deposition does not occur until the pupal case is well along in development. Color changes occur from white through pale yellow, light brown, orange, red, mahogany, to shining black. The period required to reach the shining black phase may vary from less than 3 hours (or the deposited forms already may be shining black) to more than 16 hours."

Réaumur (1742, p. 580) noted that a newly-laid larva of *Hippobosca equina* had turned chestnut color within 4 hours and was a shiny black puparium after 20 hours.

Evans (1950, p. 459) states that the mature larva of *Melophagus ovinus* becomes a puparium within 6 hours after deposition. The larva of *Pseudolynchia canariensis* does so within 2 to 3 hours, according to Coatney (1931). In *Lipoptena depressa*, the integument of mature larvae often begins to harden within 30 minutes after extrusion and the process is then completed inside a few hours;

but it may last from 6 to 14 hours for prematurely voided, yet viable larvae (Cowan, 1943).

Joly (1843), in France, noted that three female *Hippobosca equina* each deposited a larva after the integument had started to turn brown and that these puparia produced flies half an hour after deposition; an occurrence which was never reported again for any hippoboscid and is difficult to believe. Root (1921) found in the uterus of a dead *Melophagus ovinus* a puparium containing a fully-formed, dead fly. He concluded that in this instance the mother's death apparently did not arrest the pupation and the further development of the pupa into an adult. Root regarded this case correctly as abnormal, not as the normal method of pupation of *Melophagus*, as Hagan (1951, p. 160) implies. Like the other Hippoboscidae, the sheep-keed normally voids a soft third instar larva. Herman (1944) noted that occasionally in *Stilbometopa impressa* an apparently normal larva is not extruded until it has become a hardened puparium.

The foregoing occurrences are accidental and have no particular significance. There is evidence, however, that some hippoboscids normally deposit larvae at a rather advanced stage of prepupal development. Theodor (1928, p. 288), in Palestine, writes of *Lipoptena capreoli* (= *L. caprina*) as follows: "The mature larva is 2.5 to 3 mm. long, ovate, somewhat flattened, bearing at one end the shiny black spiracular plate. The remaining surface is darker brown at the wider sides and paler brown at the narrower sides. Within $\frac{1}{2}$ to 1 hour, however, the entire integument of the pupa turns uniformly shiny black and hardens. Only such pupae hatched that were already brown when voided; full-grown, white larvae of the same shape and size did not hatch, even when they blackened after deposition. The blackening of the pupa or larva does not appear to depend upon the stage of development at parturition, so that it should be interpreted as only a photochemical reaction to light. Wholly immature, small larvae, usually deposited by *Lipoptena* the first or second day after capture, blacken regularly and harden, but never hatch." Cowan (1943) made similar observations for *Lipoptena depressa*, in British Columbia, deposition of pupating larvae being apparently common in this species. He found that in the uterus the mature larva assumes a black integument and is readily discernible within the mother's abdomen; when voided, such a larva produces a normal fly. Some of the premature larvae that are laid in captivity while still white, may nevertheless pupate, but take longer to do so (in one case over 14 hours). Huzi-

matu (1938), in Japan, noted that in *Stenepteryx hirundinis* (= *S. nipponica*) the integument becomes stiff and turns mostly light-brown while the larva is yet in the uterus; it becomes a black, hardened puparium within about 2 hours after deposition. It is possible that the phenomenon is more general among the Pupipara than has been recognized thus far and that it might explain to some extent why prematurely born larvae seldom produce viable puparia, as Réaumur (1742) had observed for *Hippobosca equina*. Massonat and Vaney (1913) concluded from experiments with *H. equina* and *Melophagus ovinus* that, in these flies, only larvae which leave the mother's body after nymphosis has actually begun, will later produce flies.

A newly-laid larva is usually very delicate, even when apparently fully mature, and if handled carelessly often fails to produce a viable puparium. Coatney (1931) found that in *Pseudolynchia canariensis* it could hardly be tampered with before being several hours old, and Schuurmans Stekhoven (1923, p. 22) noticed this also for *Hippobosca variegata* (= *H. maculata*). In addition, gravid females disturbed or removed from the host, often expel premature larvae which rarely produce flies. This complicates experimental work with louse-flies, particularly when bred flies are required in fair numbers. Laboratory breeding of Hippoboscidae is always tedious and often disappointing. Helpful suggestions are given in several of the papers quoted in the present discussion of reproduction, as well as in a special article by Huff (1937) on the breeding of *Pseudolynchia canariensis*.

Duration of Pupal Development. As we have seen, the histological changes leading first to the formation of the true pupa and later to the adult, begin when the larva leaves the mother's body or shortly before. Parturition may therefore be taken conveniently as the starting point of pupal development. The end of the pupal period, however, can only be guessed at, as nymphosis may sometimes be completed and the fly ready to emerge, long before it leaves the puparium. This is particularly true for hibernating puparia, which remain alive for weeks or months before the flies appear. The following data therefore bear only on the duration of the pre-emergence or incubation period. Variations induced by external factors, such as temperature, should also be considered in this light, as it is usually impossible to determine the extent to which they might have influenced nymphal histogenesis.

Melophagus ovinus. According to Swingle (1913), in Wyoming, where summers are cool and winters severe, puparia kept on

sheep under as natural conditions as possible, give keds after 19 to 23 days in warm, and after 20 to 36 days in cold weather. Mote (1922, p. 60), in Ohio, found that emergence occurred after 10 to 14 days, the shorter period being due no doubt to the warmer summer of that area. Evans (1950), in England, determined the minimum incubation period as 20 days, the maximum as 26 and the average as $22\frac{1}{2}$, for 28 puparia obtained experimentally on sheep. Hill (1918), in Victoria, Australia, with mild winters and hot summers, had keds emerging within 22 to 24 days in winter and 19 to 21 days in spring. Graham and Taylor (1941), also in Australia, give the average pre-emergence period as 22 days, with a maximum of 30 and a minimum of 18 days, the optimum temperature for incubation being 86° F.

Lipoptena capreoli (= *L. caprina*). Theodor (1928, p. 288), in Palestine, states that the puparia give adults on the average within 30 days at 30° C.

Lipoptena depressa. In Cowan's (1943) experiments, in British Columbia, puparia, deposited by gravid females removed from the host, produced keds after 43 to 214 days, depending to some extent on the season. From those obtained from March to August, flies emerged within 43 to 140 days; while those obtained from December to February required from 113 to 214 days. It appeared that prematurely laid, but viable puparia gave keds sooner than those voided when more mature. Herman (1945) concluded from laboratory observations, in California, that the pupal incubation period may last from 6 weeks to as long as 6 months. Hare (1945b) states that, in California, "the pupal period occupies from 17 to 160 days, depending on the temperature of the incubation," and claims that the "time of emergence from the puparium is primarily determined by the total time required for pupal development. The minimum temperature at which emergence took place was 20° C." The observations on which these conclusions were based have not been published.

Hippobosca equina. In Massonat and Vaney's experiments (1913), in France, flies emerged from normal puparia after 25 days at 35° C. and within 28 to 35 days at 20° to 21° C. Carried to 700 m. above sea-level on Mt. Pilate, in southern France, in August, one puparium remained 50 days before producing the adult. The fly from Réaumur's (1742, p. 580) first puparium, voided September 18, 1740, appeared a month later (October 17).

Hippobosca variegata (= *H. maculata*). Joyeux (1915) determined that, in French Guinea, puparia produce flies from 23 to 30

days after larviposition. According to Schuurmans Stekhoven (1923), at the normal, tropical temperature of Indonesia, flies emerge on the average after $25\frac{1}{2}$ days, with a maximum of 29 days and a minimum of 22 days. It is surprising that this is about the pupal incubation period for *H. equina* in temperate Europe during the summer.

Pseudolynchia canariensis (= *Lynchia maura*). Ed. and Et. Sergeant (1907), in North Africa, recorded 23 to 27 days as the duration of pupal incubation at 42° C., the average temperature of the pigeon's plumage. In India, Adie (1915) had flies emerge from puparia after 31 to 36 days in warm weather and after 52 to 64 days in colder weather. Drake and Jones (1930), in Iowa, give 35 days as the incubation period in September. Coatney (1931), also in Iowa, had flies emerge after 25 to 31 days at laboratory temperature and somewhat sooner when the puparia were kept warmer. According to Kartman (1949, p. 127), in Hawaii, flies emerge 23 to 37 days after the larvae are deposited. In a forthcoming paper, Schuurmans Stekhoven and his co-workers, in Tucumán, Argentina, study in detail the pupal incubation period of *P. canariensis* as influenced by the seasons and particularly by the temperature. They reach the conclusion that the duration decreases from over 2 months in winter to less than one month in spring. There is much individual variation, however, regardless of the season. Even puparia deposited the same day and kept at the same temperature may show differences of up to 3 days.

Lynchia fusca. Herman (1945, p. 22), in California, reports that 7 puparia, deposited by captive flies on August 6, produced adults 49 days later on September 24.

Olfersia aenescens. Kartman (1949, p. 131), in Hawaii, obtained flies from 2 puparia 52 and 53 days after they had been produced by captive flies and then kept at room temperature.

Lynchia hirsuta. O'Roke (1930, p. 16) bred a fly from a puparium 31 days after the larva had been deposited by a female captured on a wild California quail, *Lophortyx californica*.

Stilbometopa impressa. Herman (1944) noted the exact date of deposition by flies collected on wild quail of 38 larvae voided away from the host, between August 25 and October 28. The incubation period of the only 19 adults emerging from this lot varied from 61 to 162 days. It seemed to increase with the advancing season, the average being 69.7 days for 10 puparia deposited from August 25 to September 24, and 111.6 days for 9 puparia pro-

duced from September 26 to October 28. There was, however, no sharp demarcation line between summer and winter puparia.

The European flies of swallows and swifts, *Crataerina pallida*, *Stenepteryx hirundinis*, and *Ornithomyia biloba*, which larviposit regularly in the hosts' nests, possibly produce two types of larvae. Those deposited in the early summer months develop rather rapidly, while from those produced in the fall, flies do not emerge until next year's spring or summer, sometimes several months later. The mechanism and physiology of the retarded incubation of the "winter" puparia have not been adequately studied. It is not known whether the delay is caused by a true diapause of the nymphal histogenesis or is merely due to retarded emergence of the fully-formed adult. Kirby and Spence (1826, 3, p. 101) thought that the puparia of the bird-flies were incubated by the heat of the birds sitting upon them while brooding; but there seems to be no need to assume this. Certainly overwintering puparia may produce flies in the spring even in the absence of birds. Cornelius (1869), in Germany, found in barn swallows' nests, in the fall, puparia of *Ornithomyia biloba* (= *O. tenella*) which emerged the next year from March until May. I have noted before the observations on the overwintering puparia of *Stenepteryx hirundinis* in Europe. Hardenberg (1927; 1929, p. 503), in the Netherlands, found that the summer puparia of this fly develop within 22 days; and Huzimatu (1938) says that they take 23 days to emerge in Japan (cited as *S. nipponica*). Seasonal variations in the pupal development are also recorded for the swift fly, *Crataerina pallida*, in Europe. Cornelius (1869), for instance, found that of 55 puparia collected from nests in October, some emerged indoors from the next April onward, but a few not until July, having then remained in the puparia for at least 9 months. The problem was also investigated for *C. pallida* by Büttiker (1944), who concluded that most of the puparia present in the nests in the spring emerge between June 10 and June 35, the period during which the young swifts hatch from the eggs. He also claimed that there is no second summer brood of this fly; but he failed to define the term "summer brood." Hippoboscid larviposition is a protracted performance, each female depositing in the course of the summer at several days' interval a succession of single larvae. At any time during the summer, the adult *Crataerina* population of a swift colony could therefore comprise theoretically: (a) possibly flies brought back by the returning parent birds, although we have no information on this point; (b) flies emerged from puparia that overwintered in

the nests; (c) flies emerged from puparia deposited during the current season by females of either group (a) or (b); (d) possibly flies emerged from puparia produced by group (c). It would take most careful observations and experiments to ascertain the relative numbers of each of these four groups in the total fly population at a given time. At best it might be possible to determine the time in late summer or late fall when most of the puparia become inactive to remain dormant in the nests throughout the winter. It would certainly be of interest to know how nearly this agrees with the usual time of the swifts' departure for their winter quarters. There can be little doubt, nevertheless, that the emergence of the adults of *C. pallida* is regulated by the temperature, particularly for puparia that have hibernated. By keeping winter puparia in a thermostat at a constant temperature of 16° C., Büttiker (1944, p. 29) obtained emergence about 2 months earlier than in nature (from April 10 to May 20 instead of during June).

In cold temperate regions, hibernating puparia are possibly produced also by other species of Hippoboscidae whose adults usually do not survive on the hosts during the winter. Even Réaumur (1742, p. 598), in France, noted that puparia of *Hippobosca equina* deposited in late September and in October, and kept indoors at a mild temperature, did not give flies until the next April. Roberts (1925) implies that this is true also of *H. equina* in nature in southern England, as he states that the fly appears on horses and cattle as early as April, but more often in May, and that there is a sharp falling off in numbers in late September, although a few persist into October. Johnsen (1948, p. 281) states that *H. equina* overwinters as puparia in Denmark and that flies emerged in April from puparia collected during the previous August. I have noted before that the puparia of the North American deer-ked, *Lipoptena depressa*, produced in early winter take almost twice as long to give adults as those voided in the spring and early summer.

From the foregoing data it would appear that the minimum period of pupal incubation is considerably longer in the Hippoboscidae than in the other, non-pupiparous Diptera. As Roubaud (1919) pointed out, this is true also of the tsetse-flies (Glossinidae), which emerge from the puparia in from 30 to 35 days. Roubaud correlated this with the fact that the proteins absorbed by the larva remain unassimilated in the gut during intra-uterine life, so that much time is required later in assimilating them before they can be used for the pupal histogenesis. He suggested that this explains

why the puparia of the tsetse-flies are more delicate than those of most other Muscoidea. Possibly these explanations may apply also to the Hippoboscidae; but the physiology of nymphosis has not been studied in these flies.

Individual Life Cycle. In oviparous holometabolous insects the individual life cycle comprises the egg stage, the several larval instars, the pupa, and the adult stage until the female starts to lay eggs. The duration of these several periods can generally be determined without much difficulty. This is not possible, however, in the pupiparous Diptera, where the hatching of the egg and the ecdyses between successive larval instars escape observation. The life cycle of a louse-fly, from adult to adult, comprises only two computable periods: (a) the pupal development or incubation, from the voiding of the larva to the emergence of the adult from the puparium; (b) the period covering the mating and maturation of the female and the pre-parturition time of her first-born larva.

Few attempts have been made to determine correctly the duration of the adult-to-adult cycle under optimum or at least normal conditions. The most accurate computation is that by Evans (1950, pp. 462 and 476-477), in England, for *Melophagus ovinus*. In 5 observed cases, the time between the emergence of the female and that of the fly from her first-born puparium was 33 to 36 days (34.8 days on the average); 12 to 16 of these covered the pre-parturition period (including 6 to 7 days for maturation) and 19 to 23 the pupal incubation. Graham and Taylor (1941), in Australia, had reached similar results: 20 to 21 days for the adult pre-parturition life (including 6 days for maturation) and 18 to 30 days for the pupal incubation. Different results by other investigators seem to have been due to males of various ages having been mated with newly-emerged females, the maturation periods not being the same for both sexes, as shown before. When a newly-emerged female is mated with a mature male, the female deposits her first larva after about 13 days; whereas when a newly-emerged male is mated with a newly-emerged female, the first larva is not voided until the 20th day.

From his experiments in Indonesia, Schuurmans Stekhoven (1923) calculated that in *Hippobosca variegata* (= *H. maculata*) the total life cycle took 34 to 43 days, about 12 to 14 days covering the adult female pre-parturition period and 22 to 29 days the pupal incubation.

Adult longevity. Since the Hippoboscidae produce only single larvae at rather long intervals, the average normal adult longevity,

especially of the female, is more than usually important for the population dynamics of the species. Unfortunately this is very difficult to determine for wild flies in nature, while the results of laboratory experiments cannot be applied with any degree of confidence to flies under natural conditions. Perhaps the problem could be approached by capturing large numbers of flies (particularly those of nestlings) and releasing them properly marked on wild hosts; eventually one of the marked flies might be recovered on the same or on another host. Meanwhile most of the few published statements on adult hippoboscids longevity are not based on observed facts.

Experiments with the flies of domestic animals particularly cannot be fully trusted to determine "life expectancy" in nature. The artificial conditions under which such hosts live are bound to affect the life of the parasites, enhancing their longevity in some respects while impairing it in others. Domestication no doubt protects the parasites against certain of the normal hazards of life, such as the risk of being brushed off the plumage or pelt or the failure to reach a new suitable animal after leaving for larviposition or after the host dies. On the other hand it is difficult to duplicate in a laboratory the many natural environmental factors, some of which may influence longevity in unexpected ways.

Hippobosca variegata (= *H. maculata*). In Indonesia, Schuurmans Stekhoven (1923, pp. 45-46) placed several males and females on a previously uninfested horse in a screened stable. Some of these flies survived 4 months; but no information is given from which the average longevity might be computed.

Melophagus ovinus. According to Swingle (1913, pp. 19-20), in Wyoming, female keds live from 28 to at least 165 days, or an average of 4 months. In one experiment, 6 marked, bred females, kept on sheep under natural conditions, died respectively within 36, 97, 114, 131, 137, and 150 days. In a similar experiment with 10 females, one lived 28, three 31, one 51, one 70, one 119, one 132, one at least 161, and one at least 165 days. Graham and Taylor (1941), in Australia, determined the longevity as about 80 days for the male (maximum, 105 days) and about 100 days for the female (maximum, 130 days).

Liopoptena depressa. Hare's (1945b) statement that "adults of both sexes live up to 4 months on the host," is possibly a surmise, since the evidence on which it might have been based has not been published.

Pseudolynchia canariensis (= *P. maura*). Keeping newly-bred

and previously unfed pigeon-flies in small breeding cages on pigeons, Coatney (1931, p. 527), in Iowa, found that females survived up to 28 days in one experiment and up to 48 days in another. Four males were observed living respectively 25, 29, 31, and 47 days. There seemed to be little difference in the longevity of the sexes. Since in these experiments special care was taken to protect the flies against being eaten by the birds, the average longevity under natural conditions is probably considerably smaller.

It may safely be assumed that the average adult life of the Hippoboscidae exceeds that of other, free-living, oviparous or ovoviviparous Diptera, particularly of the comparable, blood-sucking, but non-pupiparous Muscoidea. It is not so certain, however, that the females usually live longer than the males, as is sometimes surmised. Even in the case of the sheep-keel, where the experiments indicate an increased longevity of the females, it is possible that the gravid females are more exposed to accidents than the males under natural, as compared with laboratory conditions. Whether laboratory conditions in general tend to decrease or to increase the natural life expectancy is difficult to decide.

Although the Hippoboscidae live longer than most other Diptera, their life is nevertheless much shorter than that of the hosts. Lack (1943a; 1943b) determined the life expectancy in nature of the following British birds, several of which are known to harbor *Ornithomyia* in the British Isles: robin, *Erithacus rubecula*, 1 year; starling, *Sturnus vulgaris*, 1½ years; song-thrush, *Turdus eritorum*, 1½ years; blackbird *Turdus merula*, 2 years; woodcock, *Scolopax rusticola*, 2½ years; black-headed gull, *Larus ridibundus*, 2½ years; lapwing, *Vanellus vanellus*, 2½ years; and cormorant, *Phalacrocorax carbo*, 3 years. The potential life of these birds is considerably longer.

In the matter of a protracted adult life, the Hippoboscidae approach, on the whole, the blood-sucking and pupiparous, but free-living tsetse-flies (Glossinidae), where the females live from 3 to 6 months.

Rate of Reproduction. The individual rate of reproduction is the most important single factor regulating the population dynamics. In most arthropods the average number of offspring produced by a single female during her lifetime is very large, sometimes enormous; but only a small proportion eventually reaches in turn the adult reproductive stage. A clear distinction should be made, therefore, between the potential rate of reproduction, or fecundity, and the actual or final rate, the latter alone affecting the

fluctuations of the species population. The Hippoboscidae and other pupiparous Diptera are unique in that their potential rate is extremely low, due to the limited production of ova, only one of which develops at a time to the pre-puparium stage. As a result, several days elapse between successive single parturitions. Since there are bound to be in addition some losses during the free pupal stage, the actual rate of reproduction must be very small and fluctuations in the total population of the species should likewise be very slight.

The potential rate of reproduction is easily observed, either in nature or in experiments. In the Hippoboscidae it is sometimes computed from the time elapsing between successive parturitions and the average life span of a female. This method, however, does not give reliable results. Considering the very few offspring produced, it should be based on many accurate observations, which are not available at present. In the first place, the successive parturitions do not occur at regular intervals; there is evidence that reproduction is sometimes arrested or slowed down by age, at certain seasons or for other causes. Furthermore, the normal life expectancy of a female hippoboscid is not known with any precision, even for the flies of domestic animals, and is completely unknown for the wild flies.

It is sometimes believed that the maximum number of possible parturitions could be determined from the total number of developing ova present in the ovaries of virgin females. This is a fallacious method for two reasons. As explained in the section dealing with the early stages, at any one time the two ovaries of the Hippoboscidae contain a total of eight developing, unfertilized ova. This is true, not only in virgin females, but also in those that contain in addition a developing larva in the uterus; sufficient proof that after a mature ovum descends into the atrium to be impregnated, the germarium produces a new ovum, thus restoring the original number of eight unfertilized ova in the ovaries. Theoretically a female could produce more than eight puparia, provided she lived through more than eight parturitions. On the other hand, considering the duration of each single parturition, in most cases relatively few of the ova ever produce viable puparia.

The rate of reproduction should be determined accurately by observing the successive parturitions throughout the life of each of a fairly large number of isolated, bred females either previously mated or kept with a male, on a suitable host. As will be seen from the subjoined summary of published information, this method has

scarcely ever been used for the Hippoboscidae. Moreover, several of the published statements are merely surmises, without factual basis. Some are such obvious errors or guesses that it seems best to ignore them. Swingle (1913, pp. 20-21) noted several of these uncritical statements for the sheep-ked.

Melophagus ovinus. Swingle's (1913, pp. 19-20) experiments, in Wyoming, furnish even now the most reliable information on the normal potential rate of reproduction, although he worked with groups of marked females, not with isolated specimens. In a first experiment, started with 9 bred females kept on a sheep, those that lived at least 36 days averaged 2 puparia each; those living 97 days, 7.42 puparia; those living 114 days, 9.48 puparia; those living 131 days, 11.45 puparia; those living 137 days, 13.46 puparia; and the one living 150 days, 14.72 puparia. He concluded that, counting from the time the keds began to lay larvae, the average time between parturitions or needed for larval development was 7.89 days. In a second experiment, started with 12 bred females, one larva was laid by each ked on the average every 7.99 days: the average produced by each of the keds living 28 days was 2 puparia; by those living 31 days, 2.54; by those living 51 days, 4.8; by those living 70 days, 6.8; by those living 119 days, 13.26; by those living 132 days, 14.6; by those living 161 days, 15.6; and by the one living 165 days, 16.6; in the case of the last 2 keds, the rate of parturition was much decreased during the last month of their known existence, when they laid together only 3 larvae. This falling-off attributed by Swingle to senility, is most interesting, since it shows the fallacy of computing the potential rate of reproduction by dividing the total life span by the average time required for larval development, even after discounting the time preceding the first parturition. Swingle concluded that a female ked living 4 months, probably the average life span in nature, produces 10 to 12 puparia; but that some keds live at least 5 months and may then lay 16 or a few more larvae. It is clear from these findings that the number of ova observed in the ovaries of the Hippoboscidae furnishes no clue to the fecundity of these flies. Graham and Taylor's more recent work (1941), in Australia, is in close agreement with Swingle's findings. They observed that the female mates within 24 hours after emerging, but that the impregnation of the first ovum takes place only from the 5th to 6th day on, the sperm surviving meanwhile in the female's genital tract. Larval development lasts about 7 days, so that the first pre-puparium is voided 14 to 15 days after emergence, the next parturitions occurring at intervals of 6 to 7 days (exceptionally 8

days). The authors are not very clear about the total number of offspring produced during the average life span of the female. They conclude (p. 20): "The average time between pupae has been shown to be 7 days. If 100 days is taken as the average length of life of the female, and it deposits the first pupa from 14 days old, it will deposit 12 pupae during its life, while those that live up to 130 days may deposit up to 15 pupae. Actually the number of pupae produced by the females in the three longevity experiments show this calculation to be substantially correct."

Lipoptena depressa. Cowan (1943), in British Columbia, states that the gestation or intra-uterine period of a larva lasts approximately 2 months; this was concluded, not from experiments, but from having observed the first newly-emerged keds on deer in mid-June and the first mature or nearly mature larvae in females, unmistakably of the new year's crop, in mid-August. This is not convincing evidence, and scarcely warrants the conclusion that the female may produce from 4 to 7 larvae during her life span. Hare (1945b) states for the same deer-ked, in California: "The sexually mature stage of the imago is reached after about 12 days of feeding, and marked post-imaginal growth of the abdomen. After copulation, the first larva is deposited by the female on the 16th to the 19th day. Subsequent larvae are produced singly, at three-day intervals. Adults of both sexes live up to 4 months on the host, during which a female may produce up to 35 mature larvae." The evidence for these statements has not been published and they are so at variance with what is known for other Hippoboscidae, particularly for the sheep-ked, that little credence can be given them, in the absence of precise supporting data. Actually the interval between two successive parturitions and the average life span of the adult seem to have never been determined experimentally for any species of *Lipoptena*.

Hippobosca variegata (= *H. maculata*). In Indonesia, Schuurmans Stekhoven (1923, p. 39) concluded from the number of ova found in the two ovaries that a female possibly produces from 6 to 10 ova; I pointed out before that no valid conclusions can be drawn from such observations. In one of his experiments, however, 66 males and 41 females, kept on a horse in a stable, produced in one month 191 puparia, or 4.5 puparia per female.

Pseudolynchia canariensis. Coatney (1931), in Iowa, determined that 4 newly-emerged females, confined with 3 males in a small wire cage attached to a pigeon, produced within 28 days 23 larvae, or an average of 4.75 larvae per female. The flies were seen

mated on the 7th day and the first larva was voided 9 days later. In another experiment, with 7 females and 3 males, 40 larvae, or an average of 5.7 per female were deposited within 48 days, the first being voided after 8 days. The two experiments lead to startlingly different results. In the first, assuming that the female which laid the first larva on the 16th day survived until the 28th, thus laying 5 larvae in 13 days, a puparium was produced every $2\frac{1}{2}$ days; in the second, if the female which laid the first larva on the 8th day survived until the 48th, thus laying 6 larvae in 31 days, it produced a puparium every 5 days. It is, moreover, doubtful that the interval between two parturitions could be computed without knowing the life span of the several females in these experiments. I may also refer to a forthcoming paper by Schuurmans Stekhoven and his co-workers in Tucumán, Argentina, describing a series of experiments to determine the gestation time of *P. canariensis*, both of the first larva and of the next parturitions. They conclude that the first larva is voided 4 to 5 days after the newly-emerged female has mated. The intervals between the next successive parturitions seem to be shorter, varying from 3 to 4 days.

Although positive information is scant, as shown above, the normal rate of reproduction of all Hippoboscidae is obviously very low. Nevertheless, it suffices amply for the survival needs of the species. In the case of the sheep-ked, for instance, on the basis of Swingle's results, a female ked has a life expectancy of 4 months on the average and produces at least 10 puparia meanwhile. Assuming that viable adults emerge from all puparia, in about the same proportion for both sexes, the potential offspring of one female will be in the 1st generation 10 keds (5 ♀, 5 ♂), in the 2nd 50 (25 ♀, 25 ♂), in the 3rd 250 (125 ♀, 125 ♂), in the 4th 1250 (625 ♀, 625 ♂), and so on in the same progression. It should be noted that the 3rd generation will be present on the sheep within one year after the original female started feeding. Since the sheep-keds emerge on the host and since both adults and puparia are well protected in the fleece, accidental losses are probably reduced to a minimum, at least during the early stages of infestation, so that even a very low rate of reproduction assures a relatively rapid increase of the ked population on a newly-infested sheep. The two species of *Melophagus* are, however, exceptional in this respect. In the other Hippoboscidae, the puparia develop as a rule away from the host. They, as well as the emerging adults, are exposed to many risks and losses must be considerable, so that relatively few of the emerged adults reach a suitable host. No doubt this explains the very low

infestations of many bird-flies. In the case of the deer-keds, which usually occur in large numbers on individual hosts, it may be suspected that they have a higher potential rate of reproduction and possibly also a longer life expectancy in the female sex.

In conclusion, it may be pointed out that the rate of reproduction is also very low in the other pupiparous Diptera. In the free-living tsetse-flies (Glossinidae), the female produces on the average from 8 to 10 larvae during her lifetime.

(To be continued and indexed in vol. XXXIII)